THE PARTITIONING OF ENERGY BETWEEN GROWTH AND REPRODUCTION IN THE GIANT SCALLOP, PLACOPECTEN MAGELLANICUS (GMELIN)

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The Partitioning Of Energy Between Growth And Reproduction In The Giant Scallop, *Placopecten magellanicus* (Gmelin)

BY

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A thesis submitted to the School of Graduate Studies in partial fullfillment of the requirements for the degree of Doctor of Philosophy

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ABSTRACT

Populations of the giant scallop *Placopecten magellanicus* were collected from different water depths at several locations in Newfoundland. The major objective of this study was to determine whether growth and production differed between populations, and, if so, whether such differences were attributable to food availability and temperature regimes. Population reproductive characteristics such as the annual cycle of gametogenesis, fecundity, reproductive effort and reproductive *cost* were also measured to determine if they were directly influenced by environmental variables.

Additional information was obtained by examining scallops from New Brunswick and New Jersey to determine whether growth and reproductive characteristics are altered by conditions such as temperature known to vary with latitude. Scallops grown in suspended culture provided an opportunity to study age related growth and reproduction in a population of *Placopecten magellanicus* introduced to a more favourable but somewhat artificial environment.

More rapid shell growth rates, greater somatic and gamete production, and higher reproductive effort values were recorded for populations growing under more favourable conditions of food and temperature associated with shallow water and suspended culture conditions. Clearance rates and metabolic rates were well correlated with seasonal changes in environmental variables. Estimates of reproductive *cost* suggested that populations *P.magellanicus* from Newfoundland are generally *restrained* in their reproductive patterns.

Local environmental conditions strongly influenced production estimates. This is especially important in any consideration of geographical trends in growth and reproductive characteristics, as the presence or absence of such trends

appeared to depend on which characteristic was compared and the methodology used. Scallops from Newfoundland grew as fast as those collected from more southerly locations and were more productive especially when the apparent temperature advantage available to the latter populations was taken into account.

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GLOSSARY

Abbreviations

CR	clearance rate
CT	connective tissue
DG	developing gametes
GVF	gamete volume fraction
LS	lumen space
MG	mature gametes
Pg	somatic tissue production
Pr	gamete production
(Pg+Pr)	total production
RE	reproductive effort
RRV	residual reproductive value
RV	reproductive value
SWT	somatic weight
TG	total gametes

Chapter 1
INTRODUCTION

1.1. Production and Energy Balance

Estimates of production have been useful in assessing energy flow and the contributions of several species of marine invertebrates to the ecosystem (Rodhouse,1979; Griffiths,1981b). Total production consists of somatic tissue growth and the production of gametes. Observed differences in production have usually been attributed to different food and temperature regimes, but food availability has been quantified less frequently (see Bayne and Newell,1983 for review). Growth potential and reproductive potential are good indicators of the suitability of the environment, as they represent the integrated response of physiological activities in the organism. The approach often adopted has been to compare animals collected along some presumed or measured gradient of environmental stress such as the intertidal zone (Newell,1979), in addition to comparisons of populations from various environments to assess production potential for commercial exploitation (Lutz,1980; Ventilla,1982).

The influence of temperature and food on the growth of bivalves has been well documented, especially for mytilids (e.g. Widdows,1978; Bayne and Worrall,1980; Kautsky,1982a) and pectinids (e.g. Kirby-Smith and Barber,1974; Broom and Mason,1978; Vahl,1980), but with the exception of very recent studies by Bayne and Worrall (1980), Griffiths (1981b), Kautsky (1982b) and Bayne et al. (1983) their effects on reproductive output are less well known. Several studies have related clearance rates, absorption efficiencies, and metabolic rates to environmental variables in order to predict the effect on the organism's energy

balance (e.g. Griffiths and King,1979a). These rates have commonly been determined in the laboratory using phytoplankton cultures and controlled temperatures and then extrapolated to the natural conditions. Values from such studies may not be truly representive of the natural situation, and more emphasis is now being placed on measuring physiological rates in the field (Bayne et al.,1976; Newell and Bayne,1980; Kuppusamy and Ramalingam,1982) and on a seasonal basis under ambient temperature and food conditions (Bayne and Widdows,1978; Widdows, 1978; Vahl,1980; Thompson,1984b). Measurements of food availability and ingested ration are necessary for an understanding of ecological energetics in bivalves (Widdows et al.,1979; Bayne and Worrall,1980; Vahl,1980). Accurate comparison of production estimates between populations is difficult due to spatial and temporal differences in population structure (Griffiths,1981b) and the variability of such estimates is often not quantified (Broom,1983).

1.2. Growth and Reproductive Cycles

Growth rates form an integral part of any production study. Bivalves are ideal for such studies because the shell provides a record of the growth history (Seed,1976). Age and growth rate information for bivalves has routinely been obtained by analyzing shell growth increments (internal and external) or by interpreting size frequency distributions. The results of several studies demonstrating the advantages of using internal growth lines have been included in an extensive review by Lutz and Rhoads (1980).

Growth rates have often been expressed in mathematical terms by the Von Bertalanffy model which relates some measure of size (usually length) to the age of the animal. Despite some criticism (Knight,1968) the model may adequately describe growth when large numbers of animals are used and the entire size range, especially the larger animals reaching the asymptotic length, is considered. According to Brousseau (1979) the model is valuable for comparing growth in single species populations and should be valuable in determining annual growth

increments, which are essential for any age-specific production estimates. Misra (1980) and Kappenman (1981) provide methods for comparisons of such growth curves. Growth has also been described by alternative methods such as polynomial regression (Rafail,1972), which has the advantage over the Von Bertalanffy equation of rigorous mathematical testing when two or more populations are compared (Roff,1980). Advantages of the Von Bertalanffy equation include the fact that it has frequently been referred to in the literature, thereby greatly facilitating comparisons with previous studies, and the parameters describing relative growth rates (k) and maximum size ($H\infty$) have biological meaning. In this study polynomial regressions and Von Bertalanffy growth curves were fitted to the data not only for the purposes of describing growth in *Placopecten magellanicus* but also to compare the two methods. The emphasis on describing bivalve growth rates has often centred on conveniently measured shell morphometrics which may not necessarily properly describe somatic growth.

Reliable age estimates are essential for any study of bivalve growth rates , especially those describing somatic or gonad production throughout the entire life span. Stevenson and Dickie (1954) have demonstrated that the external growth rings in *Placopecten magellanicus* are laid down annually, and this has been confirmed in Newfoundland populations by Naidu (1969), but annual internal growth lines have not been described in the shells of *P. magellanicus* or other pectinids. Reasons for this may include the shell mineralogy, which for most pectinids is composed of foliated calcite and crossed-lamellar aragonite layers (Taylor et al.,1969). However, annual growth bands appear on the calcified portion of the ligament and on the resilifer depression providing an alternative method of age determination for *P. magellanicus* (Merrill et al.,1966).

Beamish and McFarlane (1983) emphasized the lack in the literature of serious attempts to validate techniques for determining age, and stress that this may result in serious errors in fisheries management and the understanding of population dynamics. There are inconsistencies not only in the formation of some

of these internal (Crabtree et al.,1980; Hughes and Clausen,1980) and external (Gruffydd,1981) growth lines in bivalves grown under similar conditions, but also in their detection in identical bivalve specimens (Crabtree et al.,1980). The majority of studies concerned with determining the precision (reproducibility) of a series of age estimates have involved fish species and have been made using the percent agreement technique, i.e. the number of times two or more observers agreed on the age they assigned to a specimen. Limitations of this method and alternative procedures have been presented by Beamish and Fournier (1981) and Chang (1982). Ideally, some indication of accuracy and precision should be ascertained for the method used to estimate age in order to obtain some degree of confidence in assigning ages to individual specimens. Inconsistencies in the formation and detection of growth increments make interspecific and intraspecific comparisons among bivalves more difficult.

Unlike other commercially important bivalve species such as oysters, clams and mussels, very little is known of the ecological production of *Placopecten magellanicus*, although several studies have provided shell growth or fisheries catch information for this species from the following areas; Bay of Fundy (Stevenson and Dickie,1954; Caddy et al.,1970),Georges Bank (Merrill et al.,1966), Newfoundland (Naidu,1969), Northumberland Strait (Jamieson et al.,1981a), off the coast of Nova Scotia (Jamieson et al.,1981b) and Gulf of St. Lawrence (D'Amours and Pilote,1982).

A problem commonly encountered in production estimates of several invertebrate species has been the measurement of somatic growth only (for review, see Warwick, 1980) while neglecting the reproductive component. This omission may result in underestimation of production and turnover ratios for bivalves by as much as 80-90 % depending on the species (Bayne and Worrall, 1980; Griffiths,1981b; Thompson, 1979,1984a). Owing to the distinct differences in reproductive output within populations between various years any study considering only one season may provide misleading results (Thompson,1979;

Griffiths,1981b). In this study the reproductive cycle and production of gametes and somatic tissue in *Placopecten magellanicus* were monitored over a three year period. The measurement of gamete output directly by induction of spawning in the laboratory (Bayne et al.,1975; Thompson,1983) or gonad weight loss on spawning have frequently been used to quantify gamete production. A prerequisite to any estimate of reproductive output is a knowledge of the reproductive cycle, especially the duration and timing of spawning(s).

Reproductive cycles of marine bivalves comprise a gametogenic phase, spawning, larval development and growth. The cycle may be annual, semiannual or continuous depending upon the species and location (Sastry,1979). Well documented patterns of energy storage and utilization are often associated with these cycles, although the role of endogenous and exogenous factors and their interactions in the synchronization of gamete development and release within populations are still not fully understood (Bayne,1976; Sastry,1979). Microscopic examination of prepared gonad material has frequently been used to divide the entire cycle into four arbitrary categories i.e., developing, ripe, spawning and spent. Separation of these categories has been rather subjective and intervals between stages are arbitrary and unequal, which leads to difficulty in statistical analysis. Recent developments in stereological techniques using a Weibel test screen applied to bivalve gonadal tissue has provided a quantitative method of comparing major events of the cycle to environmental variables (Lowe et al.,1982).

Sexes are separate in *Placopecten magellanicus* with a low incidence of hermaphroditism (Naidu,1970) and no external signs of dimorphism. Naidu (1970) described the reproductive cycle for *P. magellanicus* in Newfoundland and divided it into ten arbitrary categories based on macroscopic appearance and microscopic examination. Gonad maturation occurs from spring to early summer, and spawning takes place near the end of August or early September with the possibility of a minor spawning in June. Cycles of energy storage and utilization

have been described by Thompson (1977), who demonstrated that the energy reserves from the previous year do not play a significant role in subsequent growth and maturation of *P. magellanicus* gonads in Newfoundland. Robinson et al. (1981), working on the same species in Maine, found that the initiation of gametogenesis was dependent on stored energy reserves, although, the completion of gametogenesis utilized energy accumulated in the spring.

Several species of marine invertebrates have extensive distributions and are often found in several geographical areas. By studying populations within these areas, it may be possible to determine whether the factors that vary with latitude affect reproductive characteristics and growth. Annual fluctuation in seawater temperature has been the variable of principal concern in such studies, although a simple causal relationship has been difficult to demonstrate, partly due to the complicating effect of food availability, which has seldom been measured (Newell et al.,1982). Clear latitudinal patterns do not always emerge or necessarily hold true because localized conditions may obscure any real trends. Variations in reproductive cycles often accompany a change in latitude (Giese and Pearse,1974; Sastry,1979) such as: southern populations initiate reproduction at higher temperatures and later in the year than northern ones (Seed,1976); higher degree of synchronization of spawning in higher latitudes (Ockelmann,1958); more prolonged spawning in lower latitudes (Sastry, 1979); more restricted breeding season in higher latitudes, confined to the warmer months (Sastry,1979); and the possibility of a second spawning in the south versus only one in the north (Pfitzenmeyer,1965).

Placopecten magellanicus occurs only in the Northwest Atlantic, from the Strait of Belle Isle to Cape Hatteras (Posgay,1957). With this relatively wide distribution this species is well suited for the study of factors regulating reproductive characteristics and growth through comparative studies of latitudinally separated populations. The southern limit of distribution for *P. magellanicus* may be determined by lethal high water temperatures in summer

(Dickie,1958), whereas the northern limit may be restricted by water temperatures too low for spawning or larval development (Bourne,1964). The reproductive cycles for this species have not been described for areas other than Newfoundland (Naidu,1970), but the times of spawning throughout the geographical range have been summarized by MacKenzie (1979). Apart from some comparisons of shell growth (Dickie,1955; Merrill et al.,1966; Naidu,1969) no comprehensive study of latitudinal variation in growth exists for *P. magellanicus*. By studying *P. magellanicus* populations from distinct geographical areas insight will be gained into whether or not latitudinal trends exist in growth and reproductive characteristics.

Latitudinal studies have been used to demonstrate the possible influence of environmental factors on growth and reproductive characteristics. Food and temperature conditions may also vary with water depth. On the basis of this assumption, comparative studies have been undertaken . Several commercially important scallop species have wide vertical distributions making them ideal for such depth related studies. *Placopecten magellanicus* is no exception, as it may be collected in very shallow water ($\sim$ 2 m) near its northern limit but extends to moderate depths ($\sim$ 200 m) in the more southerly parts of its range, with variable depth patterns at intermediate latitudes. Reduced shell growth in giant scallops from deeper waters has been demonstrated in the Bay of Fundy (Brannen,1940; Caddy et al.,1970) and on Georges Bank (Posgay,1979). Other scallop species such as *Hinnites multirogosus* grown in suspended culture off the coast of California (Leighton,1979) and *Pecten maximus* in Manx waters (Mason,1957) show similar trends of decreasing shell growth with increasing water depth. All these authors attributed growth differences to food and temperature conditions; although only Posgay (1979) and Leighton (1979) provided quantitative evidence of lower food availability in deeper water. However, Richardson et al. (1982) reported that water depth had no influence on shell growth of cultured *Chlamys opercularis* from the Firth of Clyde and Gruffydd (1974b) came to the same conclusion when studying natural populations of *Pecten maximus* in the North Irish Sea.

Several species of marine bivalves such as oysters, mussels and scallops have been the subject of extensive aquaculture projects, as a result of overfishing and high market demand (Lutz,1980; Ventilla,1982). Whether factors varying with water depth affect shell growth or even production will depend on local oceanographic conditions and may be of primary interest to culturists, especially those considering suspended cage techniques. Suspending the bivalves in the water column can increase the rate at which they reach marketable size by improving food and/or temperature conditions, in addition to reducing natural predation (Lutz,1980). Scallops grown under suspended culture conditions were used as an experimental tool in this study to provide an opportunity for studying growth and reproductive characteristics under conditions favourable to the animals.

1.3. Reproductive Effort

One of the first to address the question of the partitioning of energy between growth and reproduction was Fisher (1930), who considered not only the underlying physiological mechanism but also any future consequences of particular allocation patterns for iteroparous organisms. In addition to speculating on the circumstances that may cause the organism to alter its allocation pattern Fisher (1930) also introduced the concept of reproductive value, (RV) defined as the average number of offspring a female is expected to produce during her lifespan. Williams (1966) and others proposed models to predict how natural selection would alter an organism's allocation pattern. Williams (1966) restricted the definition of reproductive value to represent current fecundity and introduced a second term, residual reproductive value (RRV), to represent the organism's future reproductive potential by taking into consideration age-specific fecundities and survival probabilities. The major assumption of the theory is that a tradeoff exists between current reproduction, growth, and survivorship due to reduced somatic investment (Bell,1984a).

Central to the theory of life history evolution is the concept of reproductive

effort, defined by Hirshfield and Tinkle (1975) as that proportion of the total energy budget that an organism devotes to the reproductive process and the costs associated with it. These authors stress the need for appropriate measurement and a proper understanding of reproductive effort in order to examine theoretical assumptions and make predictions relevant to the natural situation. Theoretical considerations of the adaptive significance of tactics or strategies which organisms utilize to budget their available resources over their lifetimes have been reviewed by Stearns (1976,1980). Accurate data concerning life cycles, resource partitioning and mortality are necessary to determine which selection regimes favour spreading reproduction over several years (iteroparity) or concentrating it into a single year (semelparity), and the adaptive value of these patterns depends on the interplay between the environment and physiological variables (Aldridge,1982). The ultimate goal of life history theorists is to understand reproductive characteristics and their variability under different environmental conditions in order to evaluate an individual's fitness expressed as the number of surviving offspring produced during an organism's lifetime.

Reproduction may have an adverse effect on the parent if some of the limited resources are diverted away from other essential metabolic processes, thereby placing the parent at risk by decreasing future survival and reproductive output (Calow,1979). Calow (1979) reviewed the literature and presented evidence of a negative causal relationship between reproductive output, residual reproductive value and parental life span in triclads, millipedes, mites, lizards and birds in addition to suggesting a quantitative method of measuring reproductive *cost*. The index of cost is zero when reproduction makes no demands on other metabolic processes, but the organism is considered *reckless* if reproduction takes place at the expense of other aspects of metabolism (i.e., a positive value for the cost index) and alternatively *restrained* if reproduction does not utilize all available energy after other metabolic expenses have been met (i.e., a negative value for the cost index).

Despite the recent increase in studies measuring reproductive effort, empirical studies involving effects of environmental factors under controlled laboratory conditions (Calow and Woollhead,1977; Woollhead and Calow,1979; Hirshfield,1980; Thompson,1983) and in field populations (Parry,1982; Bayne et al.,1983; Thompson,1984a) have been scarce. There is also a paucity of studies (Bayne and Worrall,1980; Vahl,1980; Thompson,1984b) integrating the organism's physiology and the influence of environmental factors on growth rates and absorption efficiencies, which will ultimately influence the organism's ability to exploit the available energy and partition it between growth and reproductive processes (Aldridge,1982).

Unfortunately, a uniform measure of reproductive effort has not been adopted by all workers, for the reason that the same absolute investment in reproduction can be produced by different systems of energy allocation (Tuomi et al.,1983). Methods for determining RE have ranged from simply counting or weighing gametes or gonad tissue to quantifying the proportion of nonrespired assimilation (net production) (Browne and Russell-Hunter,1978), or estimating that part of of an energy budget which is devoted to reproduction (Hirshfield and Tinkle,1975). The estimation of energy budgets or net production is often difficult and time consuming, so a more convenient ratio, clutch or gonad weight divided by parental body weight (referred to as a gonad-somatic index), has frequently been used. Several authors (Hirshfield and Tinkle,1975; Calow,1979; Thompson,1983) have emphasized the the inappropriateness of this quantity as a measure of RE, the major criticism being that two species (or individuals of the same species) may have the same ratio at equivalent body sizes but differ greatly in the absolute amount of energy gathered or in the time during which it was gathered. In order to estimate RE properly, it is necessary to determine food intake (energy budget method) or to measure accurately annual somatic growth increments (net production method), especially in animals that grow throughout their entire life (Thompson,1983). The proportion of net production devoted to reproduction provides the most informative and tangible index of reproductive

effort, at least in purely ecological terms, because it directly reflects the partitioning of energy between growth and reproduction and has the greatest potential in field studies, since measurement of food intake and metabolic loss are not required" (Thompson, 1983, page 56). However, in order to assess the consequences of a given level of effort, and whether a tradeoff exists between growth and reproduction, it is essential to establish the resource input (Calow,1979; Hirshfield,1980; Thompson,1983). Bell (1980) dismissed reproductive effort as having little importance in life history theory unless it can be related to fitness, and Goodman (1982) considered reproductive value to be a better fitness correlate, but Thompson (1983) emphasized that reproductive effort is a useful index to compare an organism's energy partitioning pattern under different environmental conditions.

Tuomi et al. (1983) raised questions concerning the established demographic theory and presented alternative concepts for reproductive effort, cost of reproduction and selection. "Demographic theory has been formulated by assuming that reproductive effort entails a fixed tradeoff between current and future reproductive success and that reproductive effort and life history traits in general are optimized by maximizing fitness under purely demographic forces of selection" (Tuomi et al.,1983, page 25). An earlier definition of reproductive effort (Williams,1966; Gadgil and Bossert,1970) also included the cost of reproduction in terms of somatic investment and implied a tradeoff which is only valid, according to Tuomi et al. (1983), when the rate of resource investment in reproduction equals the rate at which resources are drained from the soma. Many authors (Hirshfield and Tinkle,1975; Calow,1979; Tuomi et al.,1983) have suggested that an increase in resource input could uncouple somatic costs from the direct influence of reproductive effort so that somatic/survival costs need not occur. Tuomi et al. (1983) preferred to define RE as the proportion of the total investment that reproduction represents because this is a purely descriptive concept applicable in absolute and relative terms in any allocation system and does not specify a source of the investment or imply a tradeoff. Stearns (1983)

and Tuomi et al. (1983) suggested that natural selection may be operating on the whole organism by eliminating deleterious mutants and unfit phenotypes by less than perfect means as suggested by the optimal demographic theory.

Recently, numerous studies have described reproductive effort for various species of bivalve molluscs (Haukioja and Hakala,1978; Lucas et al.,1978; Thompson,1979,1984a; Bayne and Worrall,1980; Shafee and Lucas,1980,1982; Vahl,1981a; Bayne et al.,1983). When effort was measured as a proportion of net production a trend emerged from these studies whereby effort increased to reach an asymptote in some cases, indicating that the proportion of energy dedicated to reproduction increased with body size (Bayne et al.,1983). Significant variation in RE for the same species from different sites (Haukioja and Hakola,1978; Mantyla,1981 in Tuomi et al.,1983; Bayne et al.,1983) and for identical sites sampled in consecutive years (Thompson,1979; Shafee and Lucas,1980,1982; Bayne et al.,1983) was also revealed .The results emphasized the need to determine intraspecific and interannual variability in order to assess the adaptive value of particular behaviour traits (Goodman,1982).

1.4. Objectives

The objective of this study was to gain insight into the influence of temperature conditions and available ration on the production and the partitioning of available energy in *Placopecten magellanicus* in order to complement existing theoretical and experimental studies, frequently conducted under laboratory conditions. To accomplish this scallops were collected from various water depths which may be expected to represent a natural gradient of stress for this species, because conditions of food availability and temperature were shown to deteriorate with increasing depth. The animal's response to enhanced environmental conditions was examined in a scallop population grown under more favourable conditions of suspended culture. Additional insight into the variable nature of growth and reproductive characteristics of this species was obtained by observing scallop populations from the same geographical area

sampled in consecutive years and in latitudinally separated populations, and by using improved methods of assessing reproductive condition and statistical analyses of growth comparisons.

Chapter 2

MATERIALS AND METHODS

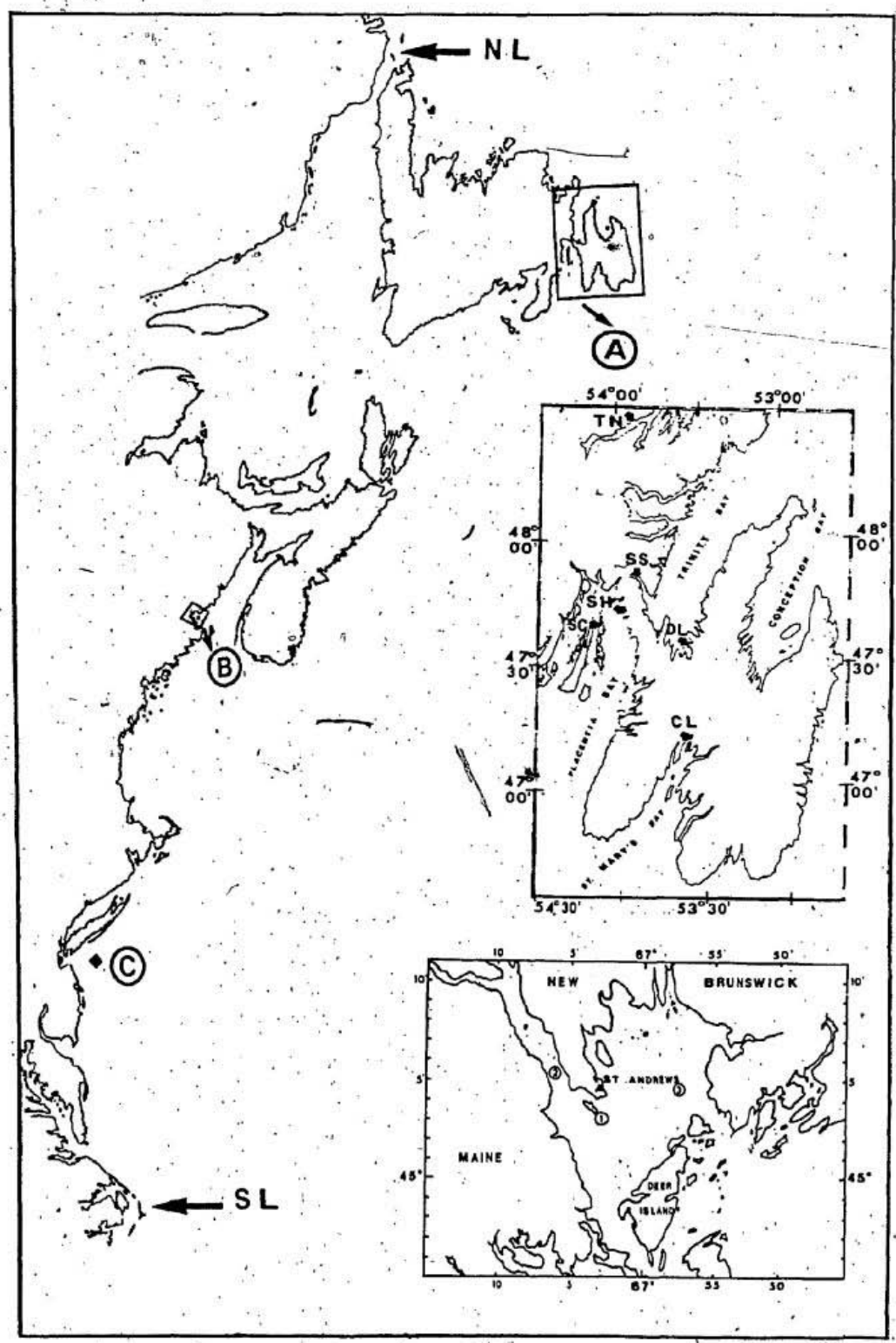
2.1. Study Sites

Scallops were collected from six locations in eastern Newfoundland by SCUBA divers and from single locations in New Jersey and New Brunswick using standard fishing techniques (Figure 2-1). The primary sites for study were Sunnyside (47°51′N,53°55′W) and Colinet (47°10′N,53°36′W) with approximate monthly collections. Secondary sites included Terra Nova National Park (48°27′N,53°56′W), Dildo (47°35′N,53°36′W), Spencers Cove (46°39′N,54°05′W), Southern Harbour (46°43′N,53°58′W), New Jersey (40°13′N,73°47′W) and St. Andrews 10m (45°03′N,67°02′W) ,31m (45°05′N,67°06′W) and 76m (45°04′N,66°57′W).

Complete size ranges of scallops were sampled from the secondary sites at least twice a year, first in August prior to spawning and again after spawning usually in October or November. Scallops from New Jersey were sampled in prespawning condition in early October and postspawning condition in November and December. Samples were routinely collected from 10m, 20m and 31m water depth with the exception of Colinet (6m,16m) and St. Andrews (10m,31m and 76m). Single depth samples were obtained from Spencers Cove (10m),Southern Harbour (10m) and New Jersey (31m).

Individual weights of gonad and remaining body tissue (somatic) were recorded after drying at 90°C for ~48 h. Measurements of shell length and height, referred to as the maximum distance between dorsal and ventral margins

Figure 2-1: Map showing locations of study sites along the east coast of North America in addition to the northern (NL) and the southern (SL) distributional limits for *Placopecten magellanicus*. Inset maps show more details of locations in (A) Newfoundland; Sunnyside (SS), Colinet (CL), Dildo (DB), Terra Nova National Park (TN), Spencers Cove (SC) and Southern Harbour (SH); (B) New Brunswick 1=10m, 2=31m and 3=76m; and (C) off the New Jersey coast .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when considering the hinge to be dorsal in position (Seed, 1980), were recorded to the nearest 0.1 mm using vernier calipers. Due to possible differences in seasonal somatic and shell growth rates only those scallops collected from primary sites between July and December were used in comparisons with secondary sites. Individual ages were estimated by interpreting shell external growth rings (Stevenson and Dickie, 1954) and growth increments on the calcareous portion of the ligament (Merrill et al., 1966).

Water temperatures were recorded by SCUBA divers using a hand-held thermometer ($\pm 0.5\,^{\circ}C$) or with anchored 180 d continuous recording thermographs (Ryan Instruments, Seattle, Wash.).

2.2. Seston Analysis

2.2.1. Collection

Duplicate water samples were obtained from three depths in Sunnyside and two depths in Colinet on approximately a monthly basis. Modified Niskin-type water samplers (~16 l capacity) were manually activated by SCUBA divers approximately 0.6-1.2 m off the bottom. Care was taken to prevent contamination by resuspension of bottom sediments by activating the sampler before the divers reached the bottom or by carrying the sampler in an upstream direction away from any disturbance before activation.

Each sampler was immediately emptied into clean buckets (~20 l) and sealed for transport back to the laboratory. Upon returning to the laboratory (within 3-6 h) each bucket was inverted several times and stirred for a few minutes to resuspend any particulate matter that may have settled. Before dividing the water into 3-4 l subsamples for chlorophyll and wet oxidation analysis, each sample was poured through a 300 μm screen.

2.2.2. Filtration

Particulate material was collected by filtering the seawater through ashed pre-weighed Whatman GF/F filters (5.5 cm diameter). The filters used for wet oxidation were washed with ~10 mls of isotonic ammonium formate prior to drying. Ammonium formate helps prevent cells from lysing and losing intracellular organic compounds but sublimes when the filters are dried prior to weighing. In the case of chlorophyll determinations, ~1 ml of a 1% magnesium carbonate solution was added to the last 100 mls of the sample. The addition of magnesium carbonate at this stage prevents the chlorophyll from becoming acid and decomposing to phaeophytin pigments.

2.2.3. Pigment Concentration

The determination of approximate concentrations of the plant pigments, chlorophylls, carotenes and xanthophylls make it possible to obtain an estimate of living plant material in the particulate fraction of seawater.

The pigments were extracted by placing the filter in 90% distilled acetone, dispersing the filter with a glass stirring rod, and following a standard procedure described in more detail by Strickland and Parsons (1972). After refrigeration for 16-20 h. the glass pulp was removed by centrifuging at a relative centrifugal force (RCF) of 3000. The extract was made up to a volume of exactly 10.0 ml using 90% acetone and the extinction values for the appropriate wavelengths were determined with a spectrophotometer when the extract was measured against a blank cell containing 90% acetone (clean filter dispersed and centrifuged). Pigment concentrations expressed as mg m^{-3} ($=\mu g\ l^{-1}$) were obtained from the set of Parsons and Strickland equations (Strickland and Parsons,1972).

2.2.4. Energy Content

The determination of the energy content of particulate material in the seawater provides an estimate of the food available to filter feeders. Wet oxidation methods have commonly been used to estimate energy content by converting oxygen demand of the organics to energy values using a conversion factor (Elliot and Davison,1975). An evaluation and detailed methodology of this technique for measuring energy content of seston was recently presented by Newell (1982). The wet oxidation method was advantageous for this study because it measured energy content directly, eliminating the need for seston conversion factors available from the literature which may vary on a geographic and temporal basis (Newell,1982).

Known weights of organic material on glass filters were oxidized to their basic elements using a known volume of a strong oxidizing agent, 2N potassium dichromate in concentrated sulphuric acid. The amount of oxidant reduced was determined by titrating the remaining dichromate against an ~0.75N ferrous sulphate solution. The following equation was used to estimate the weight of oxygen (O.C mg) required for complete oxidation of organics: $O.C = (A - B) \times N \times 8$ where A is the volume (mls) of $FeSO_4$ required to titrate the blank, B is the volume (mls) of $FeSO_4$ required to titrate the sample, N is the normality of $FeSO_4$ and 8 is the equivalent weight for oxygen. Energy content can then be calculated by multiplying O.C by 14.14 (Newell,1982).

2.2.5. Particle Size Distributions

In addition to estimating the energy available as seston, it was also desirable to determine what fraction of the particulate material was in the size range utilizable by the scallops. A Coulter Counter model Z_B was used for this purpose. According to Kranck and Milligan (1979) most suspended particulate matter falls between 1 and 100 μm in diameter. Coulter tubes theoretically function between 2 and 40% of their orifice diameter, so in order to study the desired range, two tubes (50 μm, 280 μm) with overlapping ranges were used.

Approximately every month for a twelve month period the particle size distributions in seawater were determined for three depths in Sunnyside either in the field using portable generator power or immediately upon returning to the laboratory. The quantity of particles for each respective size class was first determined using the 280 μm tube. A stirring mechanism kept the particles in suspension and blockage in the 50 μm tube made it necessary to pour the sample gently through a 50 μm screen before analysis.

With calibration information obtained using known size pollen standards it was possible to calculate particle volume and diameter for each corresponding size interval on the Coulter Counter. The data were then expressed as particle concentration by volume versus log particle size (Kranck and Milligan,1979).

2.3. Gametogenic Cycle and Gamete Volume Index

Pieces of gonad approximately 5 mm x 5 mm x 3 mm were excised from twelve scallops (6 female, 6 male) in each monthly sample from Sunnyside (10m,31m) and New Jersey (31m). The male tissues were preserved in Baker's formal calcium (+2.5% NaCl) whereas the females were usually preserved in Baker's with the exception of the period March through August when Bouin's was used to reduce damage due to egg shrinkage.

After at least 24 hours fixation, the tissues were processed through an ascending alcohol series and xylene solutions to facilitate dehydration and clearing. The tissues were embedded in Paraplast Plus (56 $^{\circ}C$) and two 7 μm sections from different depths in the block were cut on a AO Spencer No. 820 Rotary Microtome and stained by the Papanicolaou technique (Culling,1963).

The following technique, used here to estimate *volume fraction* was originally described by Weibel and Elias (1967), Freere (1967), and Briarty (1975), and modified for use with mussel gonadal tissue by Lowe et al. (1982). The *volume fraction* of scallop gonadal tissue representing the proportion of gonad

occupied by gametes (under various stages of development), connective tissue, empty follicle or other cell types, was estimated by a point count technique. This was done by examining five random fields for each section under a Zeiss compound microscope equipped with a Weibel eyepiece graticule (Graticules Ltd) under 160× magnification and extrapolating this two dimensional information to three dimensional space. This procedure is defined as stereology by Briarty (1975). To determine whether reproductive follicles were uniformly distributed throughout the entire gonad sections from the proximal (near the foot), central and distal areas of the gonad were examined.

2.4. Egg Diameter

Gravid females from 10 and 31m depth in Sunnyside were induced to spawn by placing them in seawater at ambient temperature and slowly raising the temperature by vigorously agitating and recirculating the water with a small pump. The quantity and size frequency distributions of eggs from individual scallops were determined by diluting with filtered seawater (0.45 μm) and counting on a Coulter Counter model Z_B fitted with a 280 μm tube and a channelyzer. Eggs were centrifuged at less than 1000 RCF for 10 min., washed with isotonic ammonium formate, recentrifuged, dried at 90°C and weighed. By counting and weighing the eggs it was possible to determine the weight of a known number of eggs and convert the weight values obtained for gamete production of other scallops in the same sample to fecundity estimates.

Oocyte diameters were also measured in histological sections using a microscope ocular equipped with a graduated scale calibrated with a stage micrometer.

2.5. Physiological Measurements

2.5.1. Oxygen Consumption Rates

Scallops were collected from 10m and 31m depths in Sunnyside by SCUBA divers on approximately a monthly basis between January and November 1983. The animals were kept in flowing seawater pumped directly from the ocean and maintained at ambient temperature in the laboratory until clearance rates were determined, usually within two to five days. For every monthly experiment, eight scallops from each depth, ranging in height from 135 to 155 mm, were used. The corresponding dry weight ranges for animals this size from 10m and 31m were 18-28 g and 11- 22 g respectively. Complete height ranges (n=20) of 45-174 mm (1.8-42.0 g) in 10m and 45-161 mm (0.5-25.0 g) in 31m were measured before, approximately during and after spawning at ambient temperatures. All oxygen consumption and clearance rates were determined under field ambient temperatures (for corresponding depths) in addition to laboratory ambient salinity conditions (~3.0-3.2%). Ambient levels of seston were used rather than artificial algal diets.

Oxygen uptake measurements were made in experimental chambers (Figure 2-2) similar to those described by Bayne (1971). The volumes of the chambers (C) varied from 500 mls to 4500 mls as appropriate for the size of the scallop. Seawater inflow was controlled by a valve (Vi), and after circulating through the chamber flowed to waste via a second valve (Vo) and a flowmeter (F). The centre opening was occupied by a polar graphic electrode (E) coupled to a Radiometer PHM 71 acid base analyzer (A) fitted with a PHA 934 oxygen module (M) with the output fed to a chart recorder (R). The scallop (S) was placed on a perforated glass plate (P) overlying a stirring bar (B). Water circulation was provided by a submersible magnetic stirrer (D) positioned under the chamber. The entire chamber and stirring apparatus were immersed in a temperature controlled water bath.

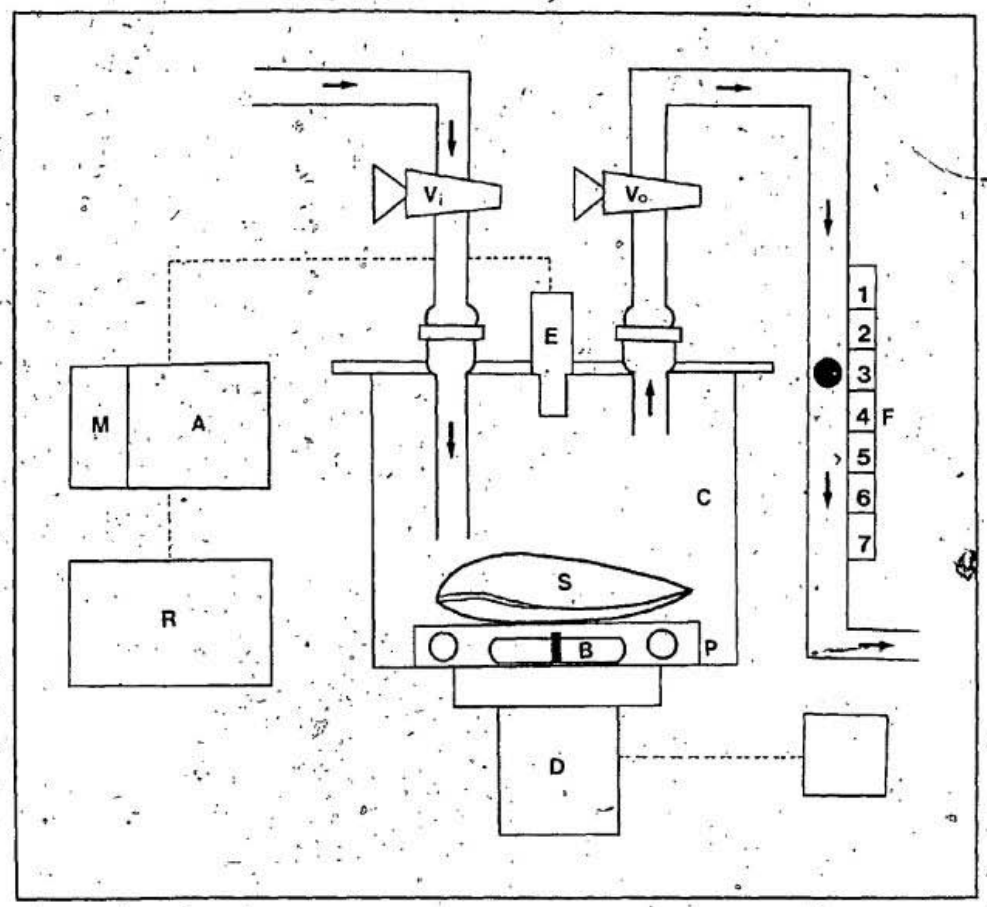


Figure 2-2: Apparatus used to measure metabolic rates for individual scallops. See text for details.

The scallops were left undisturbed in flowing seawater (80-250 ml min^{-1}) for 30-45 min. Oxygen consumption rates were measured by shutting the inflow and outflow valves, thereby isolating the chamber, and monitoring the decline of oxygen, never allowing it to drop to less than 75-80% of saturation. Each experimental run usually lasted for 30-120 min. depending on water temperature and animal size. Metabolic rates were calculated from the amount of oxygen available in the chamber and the measured pO_2 decrease. The total dry weight of soft tissues was also measured for each scallop.

2.5.2. Clearance Rates

Clearance rates were measured for the same scallops used in the metabolic rate study. The apparatus (Figure 2-3) consisted of a constant volume (~20 l) header tank (T) supplying a constant flow of water to four to 12 plastic containers (C) ranging in volume from ~0.4-4 l. Flow rates of 80-300 ml min^{-1} were used, according to the size of the scallop, such that no more than 30% of the particles were removed by the animal. Inflow was arranged so that water flowed continuously through the outflow (O), thereby providing a constant head which ensured that the flow through each valve (V) varied less than 10%. After the water entered via the inflow hose (I) it was thoroughly mixed by a stir bar (B) driven by a magnetic stirrer (M) positioned under the header tank. After the water passed through the valve it was delivered to the bottom of the container via plastic hoses (H) to where the scallop (S) was positioned and the overflow exited through the drain (D) near the surface of the container. One container was left empty serving as the inflow control (IC). The apparatus was placed in a large incubator for temperature control and during the summer months it was often necessary to pre-cool the incoming seawater.

Within an hour of placing the scallops in the containers measured volumes of water were simultaneously collected from each drain over a period of one to three minutes allowing flow rate to be determined. Particle concentrations in the control and experimental containers were determined by a Coulter Counter Model

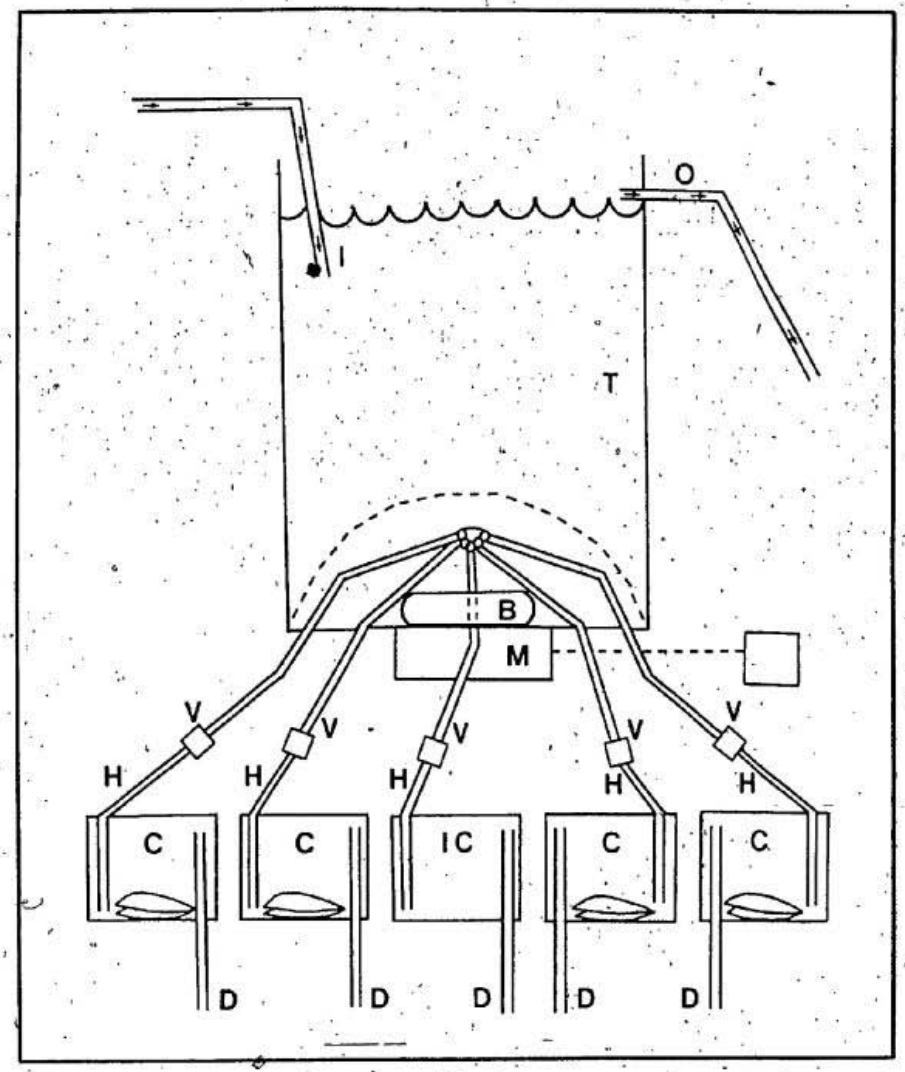


Figure 2-3: Apparatus to measure clearance rates for several scallops simultaneously. See text for details.

Z_B fitted with a 100 μm tube. The clearance rate, as defined by Bayne et al. (1976), is the volume of water cleared of suspended particles > 2 μm in diameter per unit time and is calculated as follows

$$Clearance\ Rate = F \cdot (\frac{C1 - C2}{C1})$$

where clearance rate is litres hr^{-1}, F is the flow rate of water through the container (litres hr^{-1}), C1 is the particle concentration in the inflowing water and C2 is the particle concentration in the outflowing water. The final clearance rate for each scallop was the mean of a minimum of three consecutive and consistent rates measured over a period of two to four hours.

2.6. Population Density, Spatial Distribution and Mortality

Scallop densities have frequently been determined with a scallop dredge sampling an area of bottom which may be crudely estimated. The scallop beds in this study were relatively shallow (<13 m) which permitted SCUBA divers to lay down underwater grids, which provided a much more accurate estimate of population density than is possible with dredging. To increase the visibility and reduce buoyancy each grid was constructed of white leaded rope approximately 6mm in diameter, and was secured by U-shaped iron pegs hammered into the bottom over rope junctions and by concrete blocks on the corners. The grids were subdivided into $4m \cdot 4m$ sections covering 512 m^2 (13m depth) in Sunnyside and 384 m^2 (6 m depth) in Colinet. Strips of black plastic tape 20 cm long were wrapped around the leaded line at 2 m intervals throughout the entire grid to serve as scale bars. Density estimates were determined by SCUBA divers independently counting scallops in each subdivision and recording the values on a slate.

All shell and shell fragments from scallops that died before the beginning of the study were removed from the grid. A 2 m long iron bar (with alternating 20 cm black and white sections) was placed in the centre of each $4m \cdot 4m$ section and a series of at least six overlapping photographs taken. Photographs were taken

approximately 2-3 m off the bottom using a Nikonos 3 underwater camera (28 mm lens). Enlarged black and white photographs were used to construct a mosaic of the bottom. The positions of individual scallops relative to reference points such as the 2 m scale bar, 20 cm strips of black tape, corners of subdivisions and other scallops were plotted, confirming estimates of density obtained earlier.

To approximate the distribution pattern, Hopkins and Skellam's (1954) statistic was used to test for randomness. The underlying assumption is that if the pattern is random, the distribution of the distance from a random point to the nearest scallop is identical with the distribution of the distance from a random scallop to its nearest neighbour. Thirty random points were selected (random numbers table) and distances to the nearest scallops were determined. These distances were squared and summed to represent $\Sigma\omega_1$, $\Sigma\omega_2$ representing the sum of squared differences between 30 randomly selected scallops and their nearest neighbours. The test statistic $A=\Sigma\omega_1/\Sigma\omega_2$ has an expected value of 1 if the pattern is random, whereas $A>1$ indicates aggregated distribution and $A<1$ indicates more even spacing than in a randomly dispersed population.

Mortality rates for adult scallops are very difficult to measure directly because of low natural density and great longevity. The traditional methods include measuring the ratio of *cluckers* (i.e. a pair of shells from a dead scallop that are still attached together by the ligament) to live scallops (Dickie,1955; Merrill and Posgay,1964), or estimating the relative decline in numbers of subsequent year classes (Vahl,1981a). Since neither method is totally satisfactory, natural mortality was estimated directly here by collecting the shells of animals that subsequently died during the study. By expressing the number of dead shells in each size class as a proportion of the number initially present (determined from the photographs) in that size category it was possible to construct a size related mortality curve, and integration of this size related mortality curve with scallop age estimates provided an age specific mortality curve.

2.7. Culture of Scallops

Recently a great deal of attention has been placed on the potential of commercially important bivalve species for aquaculture. Growing these bivalves under ideal artificial or natural conditions may enhance growth rates and yield. The cultured scallops for this study were from Spencers Cove and provided by the Federal Department of Fisheries and Oceans. The following shortened version of the culturing techniques was taken from Driscoll (1981). The scallops were acquired and grown under conditions of a three-phase suspension technique. The first stage was the collection of spat using suspended onion bags containing monofilament gillnet as an attachment substrate. Approximately a year later, when the spat had reached a size of about 12 mm, they were transferred to pearl nets. The normal stocking density for this second stage was 50 spat per pearl net. After a second year of growth the scallops were approximately 40-60 mm in height and ready for the final stage referred to as cage culture. The scallops were placed in compartments of lantern nets at a density of 20 per level and suspended from a head rope until the desired growth had taken place.

2.8. Comparison of Methods For Determining Age

External growth rings on the shell (Stevenson and Dickie,1954) and annual growth increments on the calcified portion of the ligament (Merrill et al.,1966) are useful age markers in *Placopecten magellanicus*. A multiple observer test was designed to determine whether either of these two methods gave more reproducible and/or more accurate results than the other and to establish the variation between individual observers in the age which each assigned to a given specimen.

Twenty scallops (43 to 164 mm in height and approximately two to 18 years old) from four locations in Newfoundland were selected using a random numbers table. Scallop shells on which external rings had been obliterated by erosion, boring organisms or calcareous algae were not included in the study. Ten

cultured scallops of known age (two to seven years) were also included. The external shell surfaces of both valves were scrubbed with a wire brush and the compressible parts of the ligament were removed from both valves to expose the underlying calcareous plate which was viewed under a binocular dissecting microscope. All four observers independently estimated the age of the 30 specimens each week using both methods ,separated by a 24 hr period. The sequence in which specimens were examined and the method employed for age determination, were reversed each week. The duration of the study was three weeks.

Extra specimens exhibiting unambiguous growth increments were used to demonstrate both methods and to ensure that readers clearly understood the following written instructions (modified from Crabtree et al.,1980)

1. Count increments from the peak to the base of the pyramid-shaped calcareous portion of the ligament (method 1) OR count growth rings from the umbo to the ventral margin (method 2). Contrast in both methods may be improved by immersing the specimen in water.

2. Count only growth increments that appear to be major ones. Use both valves of each scallop and if different estimates result record the age obtained from that valve more easily interpreted.

3. Distinctness is the most important criterion i.e., the increments with the sharpest boundaries will be the major ones.

4. In cases where increments are difficult to interpret it may help to view the specimen at arms length to try and distinguish the major boundaries.

5. Once age has been determined for a specimen do not reexamine it.

6. When using method 1 do not use method 2 for confirmation and vice versa.

7. Be consistent.

The following method of comparing the precision of age determinations (Beamish and Fournier,1981) was used to calculate an average percent error in aging the j^{th} sample:

$$\frac{1}{N}\sum_{j=1}^{N}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{X_{ij}-X_j}{X_j}\right]$$

Where X_{ij} is the i^{th} age determination of the j^{th} specimen, X_j is the average age for the j^{th} specimen, N is the number of specimens and R is the number of times age is determined for each specimen.

2.9. Calculation of Reproductive Effort, Reproductive Cost and Residual Reproductive Value

2.9.1. Reproductive Effort

The first method of calculating reproductive effort (RE), defined as that proportion of net production devoted to reproduction, required estimates of somatic and gamete production. Estimates of mean dry weight of the body tissue for each age class (i.e. somatic weight) were determined from a polynomial regression, and annual growth increments determined by subtracting the weight at any given age t from the weight at age (t+1). Age specific gamete production was obtained by first determining the appropriate shell height for each age group using the Von Bertalanffy equation $H_t=H\infty[1-e^{-k(t-to)}]$ where H_t is shell height at time t, $H\infty$ is the mean asymptotic height, k is the Brody growth coefficient and t_o is a parameter representing time when height equals zero.

Log 10 transformed values for gonad weights and shell heights were fitted to the allometric equation $y=ax^b$ where y is the gonad weight, x is shell height and a and b are fitted parameters.

Estimation of the prespawn and postspawn gonad weight versus shell height relationships made it possible to calculate age specific weight loss of the gonad on spawning providing an estimate of gamete production (Pr) where 1.0 g dry weight of eggs = 26.0 kJ (Thompson, unpubl.). Increments in dry tissue weight between subsequent year classes were used to estimate annual production of somatic tissue (Pg) where 1.0 g dry weight = 24.5 kJ (Thompson, unpubl.). The follicles in the gonads of *Placopecten magellanicus* retain their structure after spawning, unlike the mantle tissue in *Mytilus edulis* (Lowe et al.,1982). For this reason the annual increment in dry weight of the spent gonad was considered as somatic growth and added to the estimate of Pg. The organic component of the shell was not included in these calculations because it forms only 1.3% of the shell weight (own, unpubl. obs.) and represents less than 1% of the production of the scallops. Reproductive effort (RE) was calculated from the equation:

$$RE=\frac{Pr}{Pr+Pg}\cdot 100$$

when comparing age related RE of populations, the possibility exists whereby any differences demonstrated may be due to different rates of growth. An equation using the Brody growth coefficient (k) to transform the independent variable (age) and eliminate the growth rate effect has been described by Hughes and Roberts (1980). The data in my study indicated that the populations to be compared had similar k values making this treatment inappropriate and an alternative procedure was used. Size related Pr was estimated instead of age related production by determining Pr for a series of standard weight animals. Once a series of standard weights were selected (increasing by 2.5 g increments) it was possible to estimate corresponding shell heights and Pr values from polynomial equations and gonad weight relationships. Common values for Pg were obtained due to the identical somatic increment being used for all populations allowing relative estimates of RE to be calculated .

A second method used in this study to estimate energy allocation to reproduction is to express gonad output as a percentage of ingested ration (Calow,1979). Filtered ration was actually measured instead of ingested ration but due the lack of pseudofaeces production they were considered to be the same. To calculate this index for scallops from 10 and 31m depth in Sunnyside, it was necessary to correct for weight differences between scallops of similar shell heights. Clearance rates for a series of standard sized scallops were estimated with the equation:

$$CR_s = [\frac{W_s}{W_e}]^b \cdot CR_e$$

where CR_s and W_s are the clearance rate and total body weight of the soft tissues (somatic plus gonad weight) of a standard scallop respectively, CR_e and W_e are the clearance rate and total body weight of the soft tissues of an experimental scallop respectively, and b is the weight exponent. Ingested ration for standard sizes of scallops was determined for each month by multiplying the standard clearance rate by ambient levels of food availability for the respective water depths. The 1982 season was comprised of the months between September 1981 (postspawning) to August 1982 (prespawning) and the 1983 season consisted of the months between September 1982 and August 1983. The total ingestion for each year represents the sum of the monthly values. The previously determined Pr values were expressed as a proportion of the total annual ingestion in each season for several standard sizes of animals. Using the same techniques it was also possible to express Pg and oxygen consumption as a proportion of ingested ration. For additional comparisons total weight of the soft tissues was converted to the appropriate age for each group in each year.

2.9.2. Reproductive Cost

Calow's (1979) index of *reproductive cost* represents the proportion that reproduction drains from the nonreproductive metabolic demands of the parent and may be expressed as,

$$\textit{reproductive cost} = 1 - [\frac{(C \cdot e) - Pr}{R^*}]$$

where C is the ingested ration , e is absorption efficiency, Pr is energy allocated to reproduction and R* is the metabolic demand of the somatic tissue (N.B. Calow's original notation is different).

Bayne et al. (1983) modified the index by incorporating a term R - R* where R is total metabolism, which can be directly determined.

$$reproductive\ cost = 1 - \left[\frac{(C \cdot e) - (Pr + R - R^*)}{R^*}\right]$$

R* was estimated using a similar technique to that described by Thompson (1984a) whereby the annual metabolic cycle was divided into gametogenic and non-gametogenic phases. The non-gametogenic phase was delineated by criteria such as relatively low gamete volume index values and minimal values for gonad weight, indicating reduced gametogenic activity. From the oxygen consumption rates during the non-gametogenic phase a mean metabolic rate for somatic tissue demand was calculated and applied to the entire year (1 ml O_2=19.9 J).

2.9.3. Residual Reproductive Value

Residual reproductive value (RRV) for a given age represents an organism's future reproductive potential by taking into consideration age-specific fecundities and survival probabilities. In this study RRV was expressed in terms of energy expended in gamete production rather than fecundity (numbers of gametes), using the following equation

$$RRV = \sum_{t=x+1}^{\omega} \frac{l_t}{l_x} m_t$$

where l_t/l_x is the probability of survival from age x to age t, ω is the age of last reproduction and m_t is gamete production at age t. A life table of l_t/l_x survivorship probabilities was constructed using the mortality data from the density study.

2.10. Statistical Analysis

A linear form of the allometric equation $y=ax^b$ may be obtained by transforming both variates to logarithms and fitting the data by least squares regression to a straight line $Log_{10}y=Log_{10}a+bLog_{10}x$ (Snedecor and Cochran,1972). This technique has been used throughout the study to describe relationships between clearance or metabolic rates and total body weight, and between gonad or somatic weights and shell height.

Polynomial regression, a form of multiple linear regression, was used to describe the relationship between shell height or somatic weight and age. A polynomial regression may be described by the following equation: $y=\beta_0+\beta_1x+\beta_2x^2+\beta_3x^3 \ldots.\beta_mx^m+\epsilon$ where β_0, β_1, $\beta_2 \ldots. \beta_m$ are population parameters, y is the value for x and ϵ is random error at observation x (n.b. $\beta_0 = \alpha$ in Zar's (1984) notation). According to Zar (1984) it is necessary to determine the maximum power of the polynomial that has significance. One usually proceeds by fitting a small model then increasingly larger models, e.g. one fits a simple linear equation $y=\beta_0+\beta_1x$ to the data, then adds an additional term β_2x^2 producing a quadratic or second degree polynomial.

In an analysis such as polynomial regression multicollinearity is a problem i.e. there is usually a strong linear relationship between regressors (x^2,x^3, etc). This results in the affected estimates being unstable and possessing high standard errors. A technique described by Neter et al. (1983 p. 319), in which the value of x is replaced by $x-\bar{x}$ to reduce multicollinearity substantially, was used throughout the study. One of the criteria used to determine if the addition of the quadratic term improved the prediction of y values was to test the null hypothesis $H_o:\beta_2=0$. If this hypothesis was accepted then the addition of the quadratic term did not significantly improve the fit, indicating that the simpler linear model was adequate. However, if the null hypothesis was rejected then an additional cubic term β_3x^3 was introduced to the quadratic equation and tested to determine if a significant improvement was obtained. These terms were added until $H_o:\beta_m=0$

was accepted and the conclusion was that the best fit was obtained with a polynomial of degree m-1.

Analysis of variance (ANOVA) tests the equality of population sample means by determining whether the variance between samples being tested is significantly greater than the variance within samples. In order to determine the effect of a single factor on population means a one-way ANOVA was used in this study, and to determine simultaneously the effects of two factors and the interaction among factors on population means a two-way ANOVA was performed. For data expressed in the form of a proportion (or percentage), the arcsin transformation was carried out (arcsin(sqrt argument)) before ANOVA was used.

Regression equations were fitted to a variety of data from different scallop populations in order to demonstrate the strength of the relationships between variables and to predict a value for the dependent variable within the range of observed values for the independent variable. Direct comparisons between regressions were also made. In order to determine if the populations being compared had the same regression parameters (slope and intercept), an analysis of covariance, which combines the methods of regression and analysis of variance, was used. When comparing regression equations dummy variables were introduced to the model to incorporate the test equations into a single equation to allow analysis and to test the significance of coefficients. A modification described by Neter et al. (1983) was also used to reduce correlation between the dummy variable and dummy times x. The heterogeneity of slopes was first tested, and if the slopes were significantly different at the predetermined significance level (usually $P<0.05$) then the analysis was complete, i.e. the samples came from different populations. However, if the slopes were not significantly different then a common slope was calculated from the samples and a comparison of the elevations was made. If the elevations were different the analysis was complete whereas if the elevations were similar a new common regression equation incorporating all the samples was calculated.

When comparisons of more than two samples were required it was necessary to use a different approach than simply comparing all possible pairs of samples using two-sample tests. According to Zar (1984) the use of two-sample techniques to solve a multisample problem is invalid because the chances of making a Type 1 error (rejecting the null hypothesis when it is true) increases with the number of samples being compared. When multiple comparisons were performed an improvement on the test was made using the Bonferroni approximation, which simply divides the significance level by n before rejecting the null hypothesis. This reduces the possibility of a Type 1 error and makes the test more conservative.

The General Linear Model (GLM) procedure of the Statistical Analysis System (SAS Institute Inc.) was used to compare regressions and for analysis of variance, whereas the Nonlinear procedure (NLIN) was used to construct the Von Bertalanffy model and to test the parameters. Experimentation with the options in NLIN revealed that the Marquardt algorithm usually provided the most consistent iterations, with narrow confidence limits for the parameters and rapid convergence, so this method was used throughout. Comparisons between homologous parameters in sets of Von Bertalanffy equations were made by inspection of the 95% confidence intervals for the appropriate dummy variable in the model. If the interval crossed zero, the null hypothesis was accepted, i.e. the coefficient for the dummy variable was not significantly different from zero and the values for the parameter in the comparison represented by the dummy variable were therefore not significantly different from each other. It should be recognised that strictly speaking this test is valid only if the F-distribution applies, which is not known for these data, but this restriction also holds for the calculation of the confidence limits produced by the NLIN procedure in SAS for the parameter estimates in nonlinear models, so that no further assumptions are being made when Von Bertalanffy curves are compared. Furthermore, comparisons of the same data sets fitted by polynomials, which can properly be examined by linear methods, provided similar results to those of the nonlinear

(Von Bertalanffy) comparisons in almost all instances (Sections 3.6.1 and 3.6.2), suggesting that the latter are robust, at least for the scallop data obtained in this study. It seems likely that this robustness is attributable in part to the large sample sizes used.

Chapter 3
RESULTS

3.1. Environmental Conditions

3.1.1. Seawater Temperature

At Sunnyside the temperature increased from a minimum value of -1.0 to -1.5 °C during February to April to a maximum of 12-14 °C in the shallowest water in September (Figure 3-1). The temperature then decreased during autumn and early winter due to a decline in the effects of the summer heating cycle on the surface water. The temperatures in Colinet never dropped below zero in the winter and reached a maximum of 17 °C in August. The water temperature was higher in the shallowest depths sampled at each site with the exception of the winter period (approximately January to April) when the water column was vertically uniform. During the summer a thermocline in less than 20-30 m at Sunnyside resulted in vertical stability and the greatest temperature differential between water depths.

Data for sampling depths at St. Andrews, New Brunswick were obtained from Forgeron's (1959) investigation and the points on the figure represent average monthly temperatures for the 1957 and 1958 seasons. The QP stations #5(53m), #8(22m) and #7(24m) described in Forgeron (1959) closely correspond in position and depth to the collection sites #3(76m), #2(31m) and #1(10m) respectively in this study . An approximate estimate for the water temperature at 10m depth for QP station #7 was calculated by averaging the temperatures recorded at the surface (0m) and the bottom (24m).

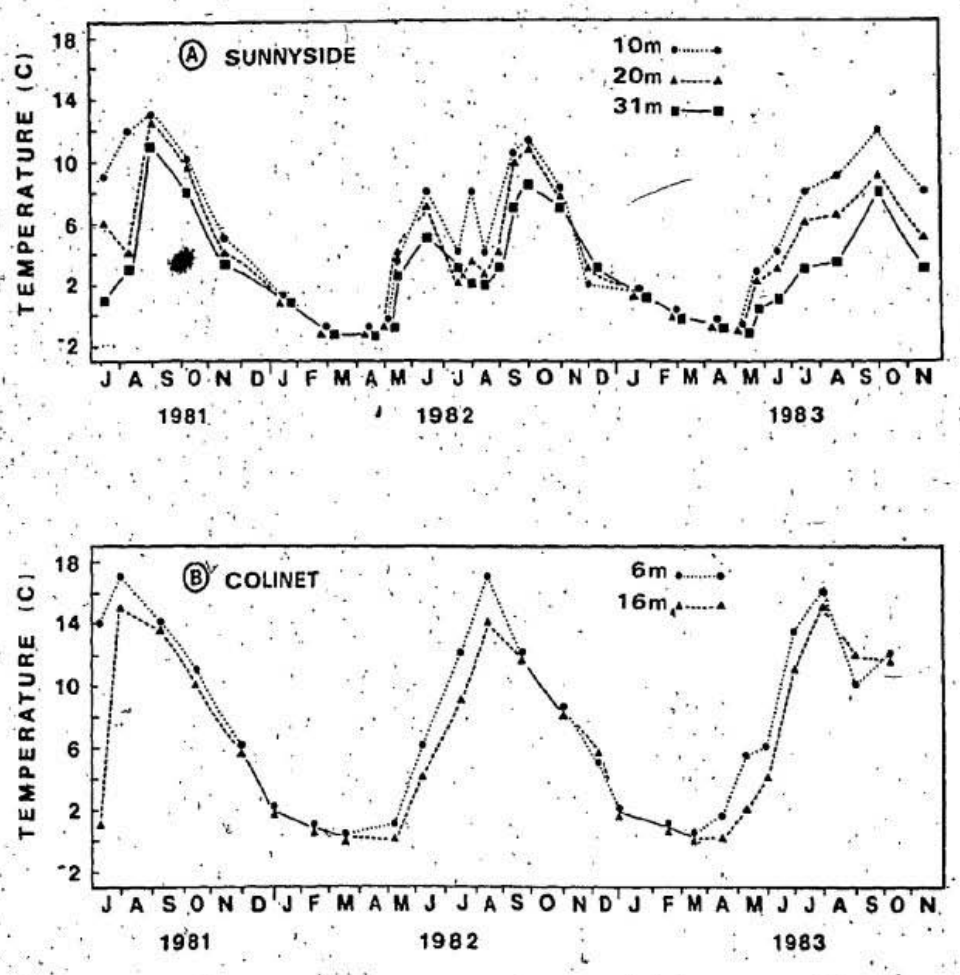


Figure 3-1: Seasonal temperature cycles at various depths in Sunnyside and Colinet.

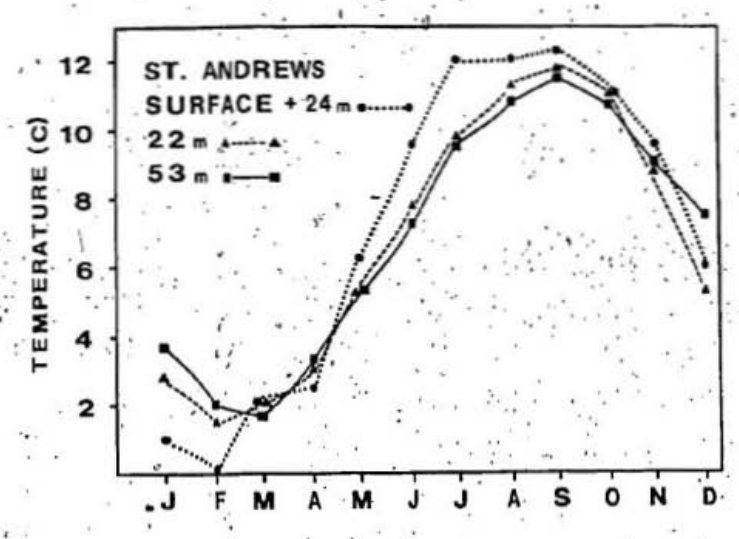


Figure 3-2: Seasonal temperature cycles for three water depths in St. Andrews, New Brunswick.

Water temperatures at St. Andrews were very similar in 22m and 53m and ranged from 2 to 11.5°C (Figure 3-2). The temperature estimate for the surface and 24m depth combination was lower than the other samples during January and February when it dropped to 0°C but was similar to them from March to May. The temperature estimate for the shallow water combination was greater than the other samples from June through August and reached a maximum of 12°C before temperatures for all three samples declined during October and November.

3.1.2. Annual Day Degrees

Estimates of annual day degrees in the various years at each water depth were obtained by multiplying the monthly temperature value by the number of days in the month and summing these values. For the purpose of this study the values are expressed in positive day degrees because the temperature dropped below zero during the winter in Sunnyside resulting in the negative day degrees being subtracted from the total.

Total annual day degrees decreased with water depth at Sunnyside, Colinet and Terra Nova National Park (TNNP) as follows:

Dep(m)	Sunnyside		Colinet		TNNP	St. Andrews	
	1982	1983	1982	1983	1983	1957	1958
6	-	-	2334	2388	-	-	-
10	1404	1497	-	-	1530	2521	2551
16	-	-	2004	2112	-	-	-
20	1239	1314	-	-	1461	2340	2460
31	1014	900	-	-	828	-	-
53	-	-	-	-	-	2385	2550

Whereas the number of annual day degrees at TNNP and Sunnyside were similar, there were fewer than for either depth at Colinet. Annual day degrees were similar between the two years despite great fluctuations in individual monthly temperatures e.g., in 10m depth at Sunnyside during July and August.

Temperatures were slightly lower in 1958 at St. Andrews but differences between depths for any particular year were less than 10% and were occasionally nil i.e.,10m and 53m in 1958.

3.1.3. Chlorophyll a Concentration

In Sunnyside pigment concentration was lowest in the winter with a sharp increase during the spring bloom in April or May, reaching maximum values of approximately 5.5 $\mu g\ l^{-1}$, and relatively high concentrations in the shallower depths from July to September (Figure 3-3). A similar trend may have occurred in Colinet but owing to heavy ice formation routine sampling in the winter/spring was prevented probably resulting in insufficient information on the spring bloom.

With a few exceptions chlorophyll values in Sunnyside and Colinet declined with increasing water depth. Chlorophyll concentrations in 31m at Sunnyside were consistently low, usually less than 0.5 $\mu g\ l^{-1}$, during the entire study with the exception of the spring bloom and a month or two immediately after the bloom. Values from 10m in Sunnyside were consistently higher but more variable from month to month than those from other depths studied, the concentrations from 20m usually falling between the 10m and 31m values.

With the exception of the apparent lack of spring bloom data from Colinet in 1982 the absolute values and seasonal trends of chlorophyll concentration in Sunnyside and Colinet were similar. The major differences between the 1982 and 1983 seasons were the more intense spring bloom in 1982 (although the bloom occurred at the same time each year) and the higher chlorophyll values in the winter of 1982-1983 compared with 1981-1982 for all depths except 31m.

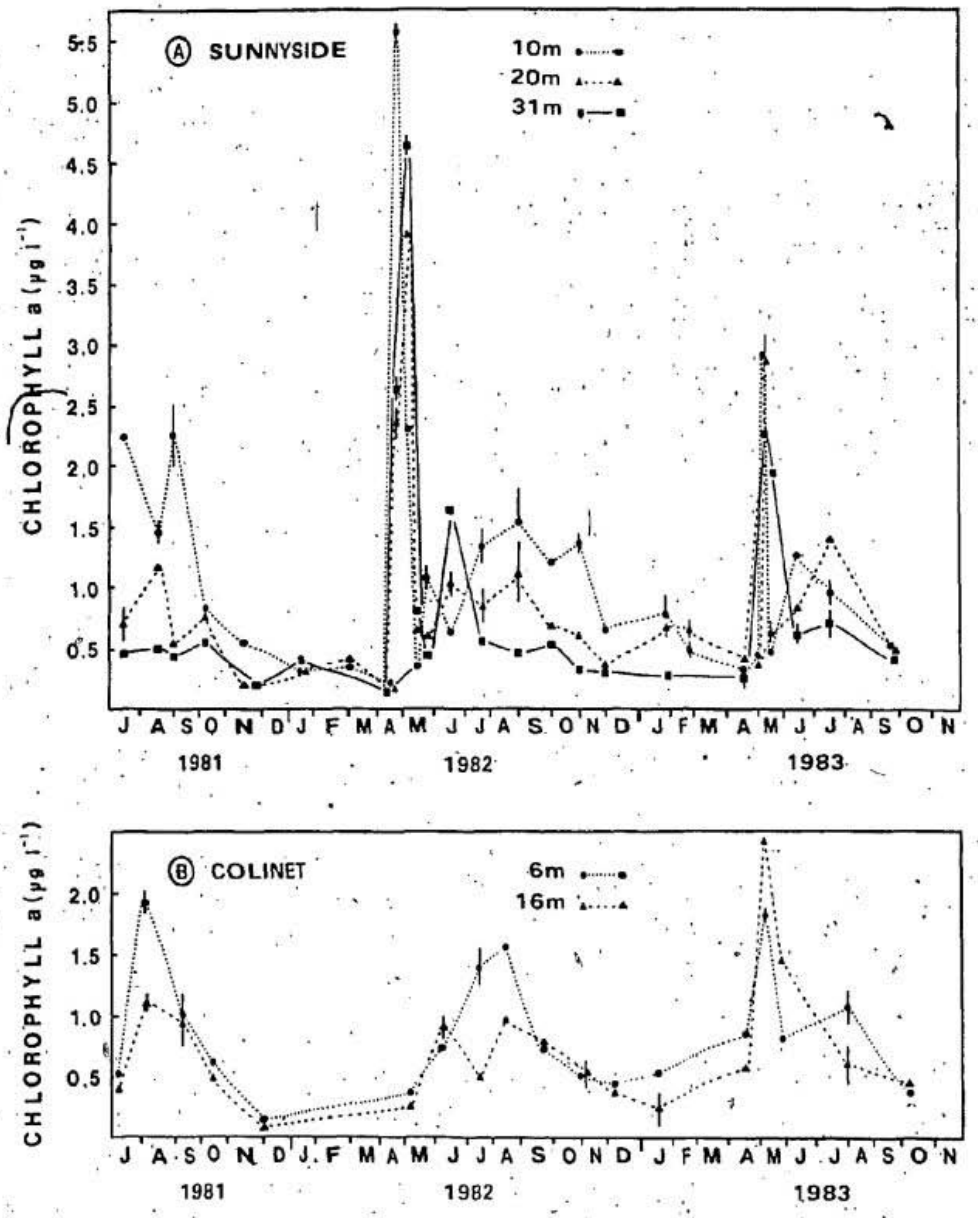


Figure 3-3: Seasonal cycles of chlorophyll concentration in Sunnyside and Colinet. Symbols represent mean values and range of the estimates.

3.1.4. Food Availability

Minimum values of approximately 10-15 J l^{-1} generally occurred in winter, increasing markedly during the spring bloom to 65 - 75 J l^{-1}, but unlike the chlorophyll data maximum values were found in the deeper water (Figure 3-4). Relatively high values of 30 - 50 J l^{-1} were also seen in the late summer and autumn. These values were similar to those reported for the Long Island NY area (Newell et al., 1982).

Whereas energy content of seston was greater in the shallowest water from Sunnyside during the earlier half of the study, no consistent depth pattern was seen during the second half of the study, or in the Colinet data. A technique similar to the one used to calculate day degrees was used to integrate the areas under the lines in Figure 3-4 in order to obtain an index of the food available at each depth during the 1982 and 1983 seasons. Thus the monthly value of food availability for each depth was multiplied by 30 and summed to give an estimate of annual food availability (cumulative day Joules per litre). These relative indices of food availability for Sunnyside and Colinet during the 1982 and 1983 season are:

Dep(m)	Sunnyside		Colinet	
	1982	1983	1982	1983
6	-	-	6795	6765
10	9052	6955	-	-
16	-	-	6315	6600
20	7917	7565	-	-
31	5752	7195	-	-

A decrease in day Joules with depth was evident in the 1982 Sunnyside data but the difference was not as distinct in the Colinet data. In 1983 annual day Joules were greater in 20m than in 10m at Sunnyside, but differences between depths were slight, and values were lower than in 1982. In general, values for day Joules in Colinet were similar to those from 31m in Sunnyside but less than those from equivalent depths in Sunnyside.

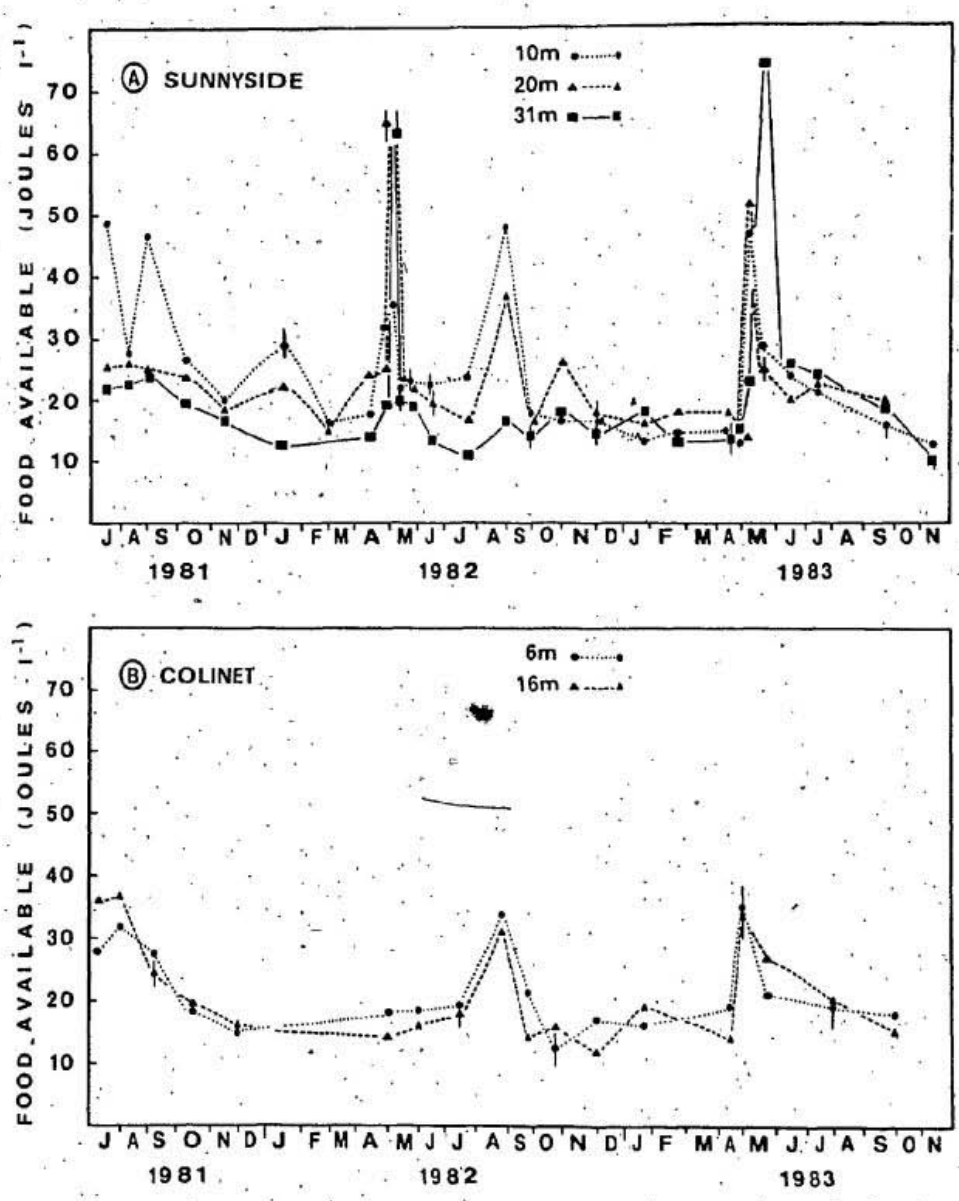


Figure 3-4: Seasonal cyle of particulate energy content in Sunnyside and Colinet. Symbols represent mean values and range of the estimates.

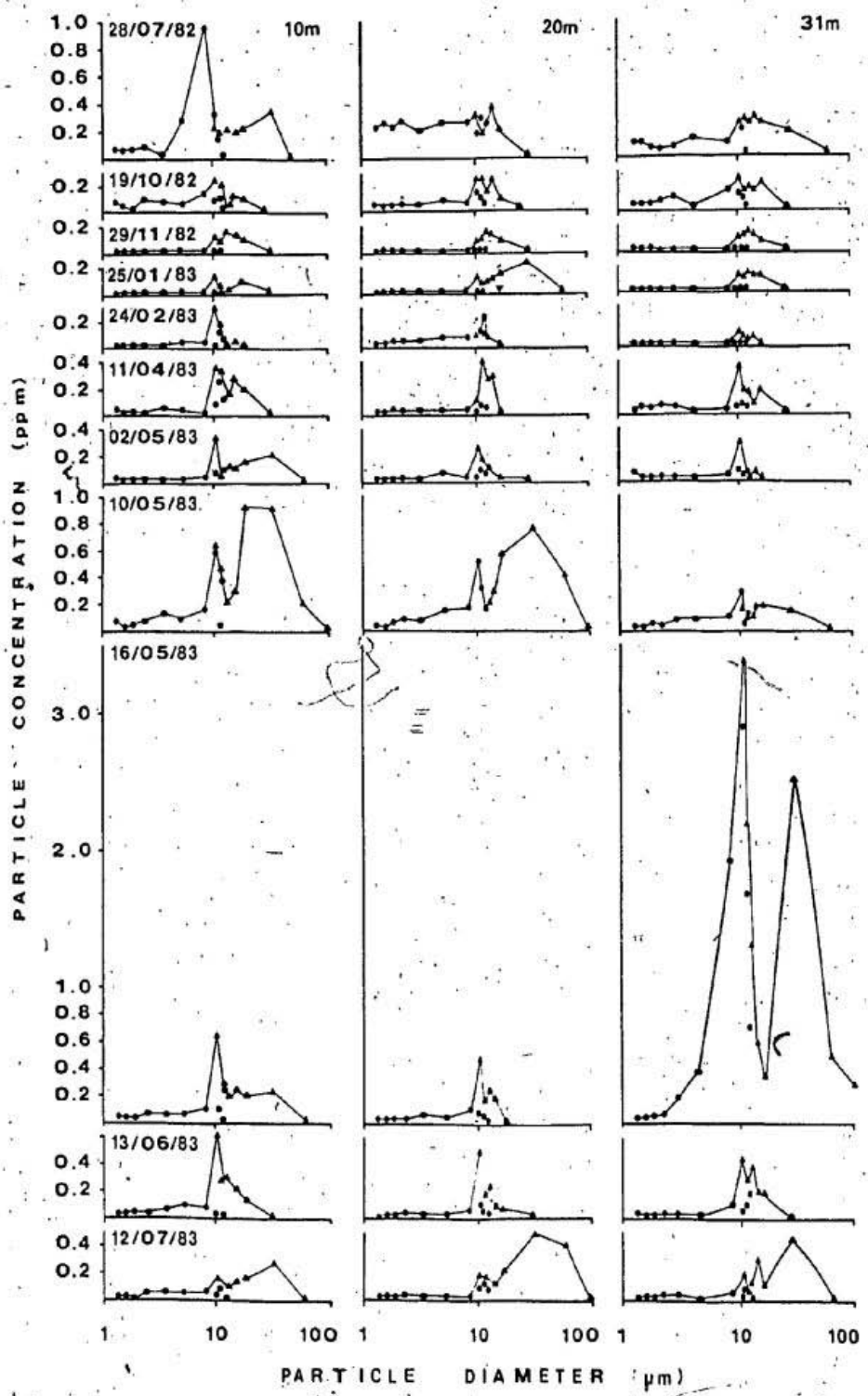
3.1.5. Particle Size Distributions

A classification scheme consisting of four basic particle distribution types found in the marine environment (Kranck,1980) was used to describe the particle size distributions from Sunnyside seen in this study. In July 1982, the distribution seen in 10m could be described as a Type A or bloom spectrum, which has one or more sharp peaks comprising over half the volume and consisting predominantly of living phytoplankton plus low background levels consisting of other particles such as miscellaneous plankton cells and detritus (Figure 3-5). The distributions seen in the 20m and 31m samples for the same date could be described as Type C or mixed spectra consisting of a mixture of plankton or detritus having one or more plankton peaks superimposed on a poorly sorted background material. Alternatively, the 20m and 31m spectra could be regarded as Type D, or flat spectra, characterized by low total concentrations with similar volumes for all sizes of particles and consisting mainly of living cells with the presence of some detritus.

The particle distributions between October 19, 1982 and May 5, 1983 appeared to be the mixed type with a few plankton peaks, or alternatively the flat type. There was little difference between depths. During this time of year the water column is vertically homogenous, resulting in similar temperature and energy content values, although the chlorophyll values appeared to be higher in 10m and 20m than in 31m.

On May 10, 1983, the distributions in 10m and 20m are bloom spectra, whereas a mixed spectrum appears evident in 31m. At this time chlorophyll values had greatly increased, indicating that the spring bloom had begun at water temperatures near zero. Almost a week later, on May 16, the volumes of the distributions in 10m and 20m had dropped considerably as had the chlorophyll values, but the patterns may still have met the criteria for bloom spectra. At this time a major difference between water depths became apparent as particle volume greatly increased in 31m, chlorophyll concentration remained high and a very

Figure 3-5: Particle size spectra for water samples collected in three depths at Sunnyside during 1982 and 1983. Triangles represent values obtained with the 280 μm tube and circles obtained using the 50 μm tube.


28/07/82
10m
20m
31m
19/10/82
29/11/82
25/01/83
24/02/83
11/04/83
02/05/83
10/05/83
16/05/83
13/06/83
12/07/83
PARTICLE CONCENTRATION (ppm)
PARTICLE DIAMETER (μm)
1
10
100

marked bimodal spectrum was seen, indicating that the phytoplankton bloom was still in progress in the deeper water.

During June and July 1983 there were no great differences in spectra types between water depths. They may be classed as either mixed or bloom spectra, but again the chlorophyll values were highest in 10m and 20m. The particle size distributions observed in this study were similar to those profiles described by Sheldon et al. (1972) for several areas in the western North Atlantic, where particle size distributions in the surface water often displayed bloom or mixed distributions and varied from place to place, whereas relatively flat uniform distributions were characteristic of deeper waters (>50m).

3.2. Reproductive Characteristics

3.2.1. Annual Cycle of Gametogenesis

Gamete volume fraction (GVF) was measured in two females and males (collected in July 1981) using sections taken from three different places in the gonad. There was no significant difference in GVF between males and females ($F=1.35$, $df=11,48$, $P<.25$), position in the gonad ($F=0.40$, $df=11,48$, $P<.84$) or in the interaction factor ($F=1.24$, $df=11,48$, $P<.31$). For the purpose of this study the gametes seen in histological sections of *Placopecten magellanicus* gonads were divided into two categories: 1) developing, representing the earliest stages; and 2) mature, representing the gametes proper (Figure 3-6). Separation of the gametes into two categories was less subjective in the males, where spermatozoa were easily distinguished from the larger spermatogonia and spermatocytes. In the females, however, it proved difficult to separate oocytes in the later stages of growth from those which were mature.

Seasonal cycles in volume fractions for developing gametes (DG), mature gametes (MG), total gametes (TG), connective tissue (CT) and lumen space in the follicle (LS) were determined for scallops from 10m and 31m at Sunnyside (Figures 3-7, 3-8).

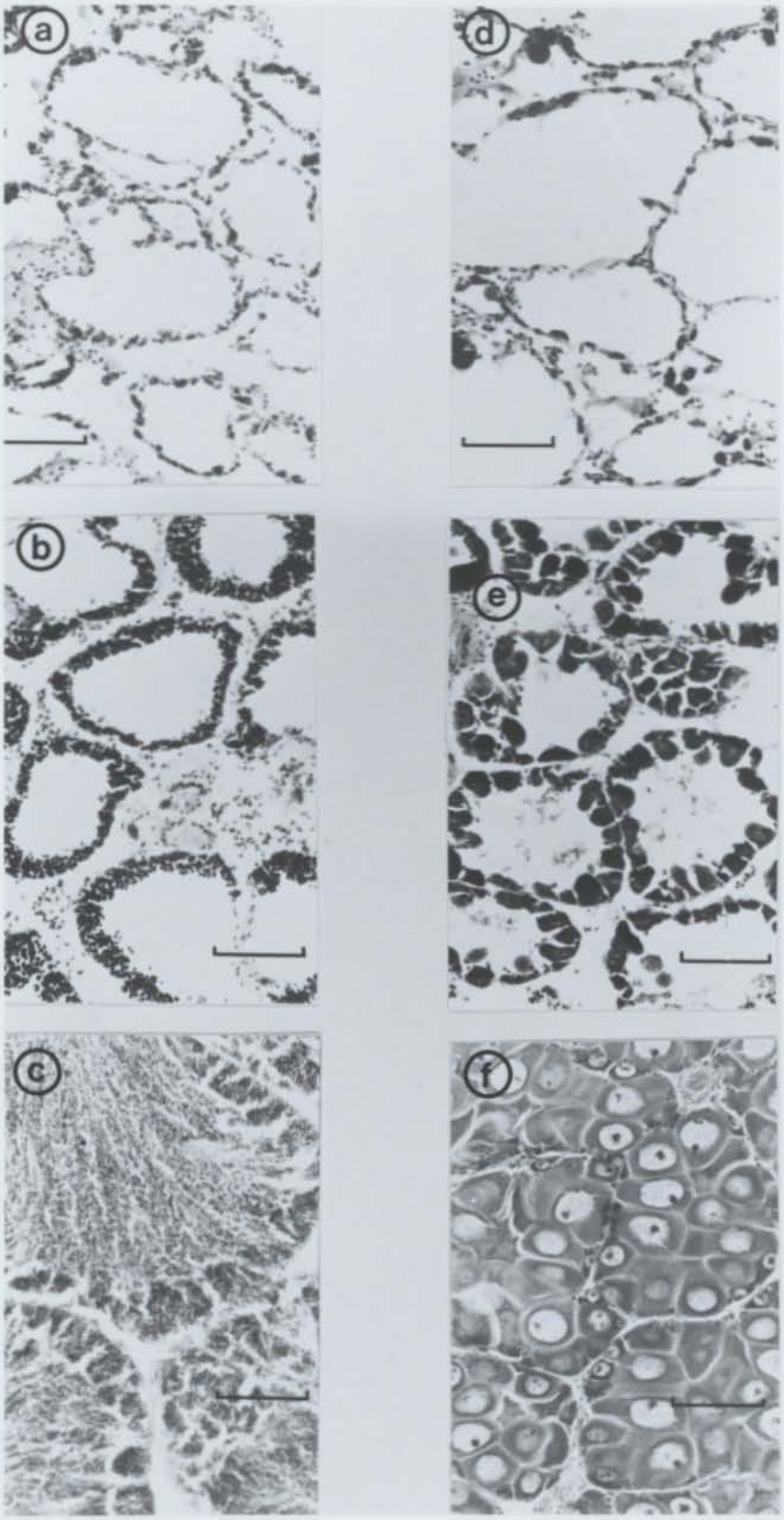
Minimum values of approximately 20% for the total GVF of males and females combined were observed between October and December, just after spawning in late August or early September (Figure 3-7). Maximum values of 85-95% for total GVF occurred between June and August. Minimum values of GVF for mature gametes in each sex approached zero from October to April and reached a maximum of 50-70% in the males and 75-95% in the females during July and August (Figure 3-7). The higher value for the females could be an overestimate due to the difficulty in distinguishing between mature and developing oocytes.

The rapid increase in total GVF between December and April is largely due to an increase in the percentage of both male and female developing gametes (Figure 3-8) during the same period when fully developed gametes were not present. The maximum values for the percentage of connective tissue in the gonad were approximately 35-55% and occurred in October and November with minimum values of 5-15% in July and August. Empty follicle space showed a similar trend with respect to the timing of minimum and maximum values but the maxima never attained the high values observed for connective tissue. The maximum values for these sets of percentages corresponded to minimum values for total gametes and vice versa.

The time of spawning was similar to that reported by Naidu (1970) and Thompson (1977) for *Placopecten magellanicus* in Newfoundland but there was no indication of a second (minor) spawning in June as observed for a population from the west coast of Newfoundland (Naidu,1970).

Scallops from 10m and from 31m at Sunnyside spawned during August in 1981, 1982 and 1983 (Figure 3-7). With the exception of April 1982 the total GVF was consistently higher in 10m than 31m. Two-way analyses of variance (ANOVA) revealed that there was no significant depth effect for the remaining portion of the 1981 calendar year or in the interaction term depth*month but that the month factor was highly significant. In the calendar years 1982 and 1983

Figure 3-6: Photographs of three stages of development in male and female gonads. Development in the males and females respectively are seen in a and d, those representing the condition of the gonad immediately after spawning. Fields b and e display developing gametes only, and c and f are from scallops collected in June, displaying both mature and developing gametes. Scale bars represent 100 μm.


a
d
b
e
c
f

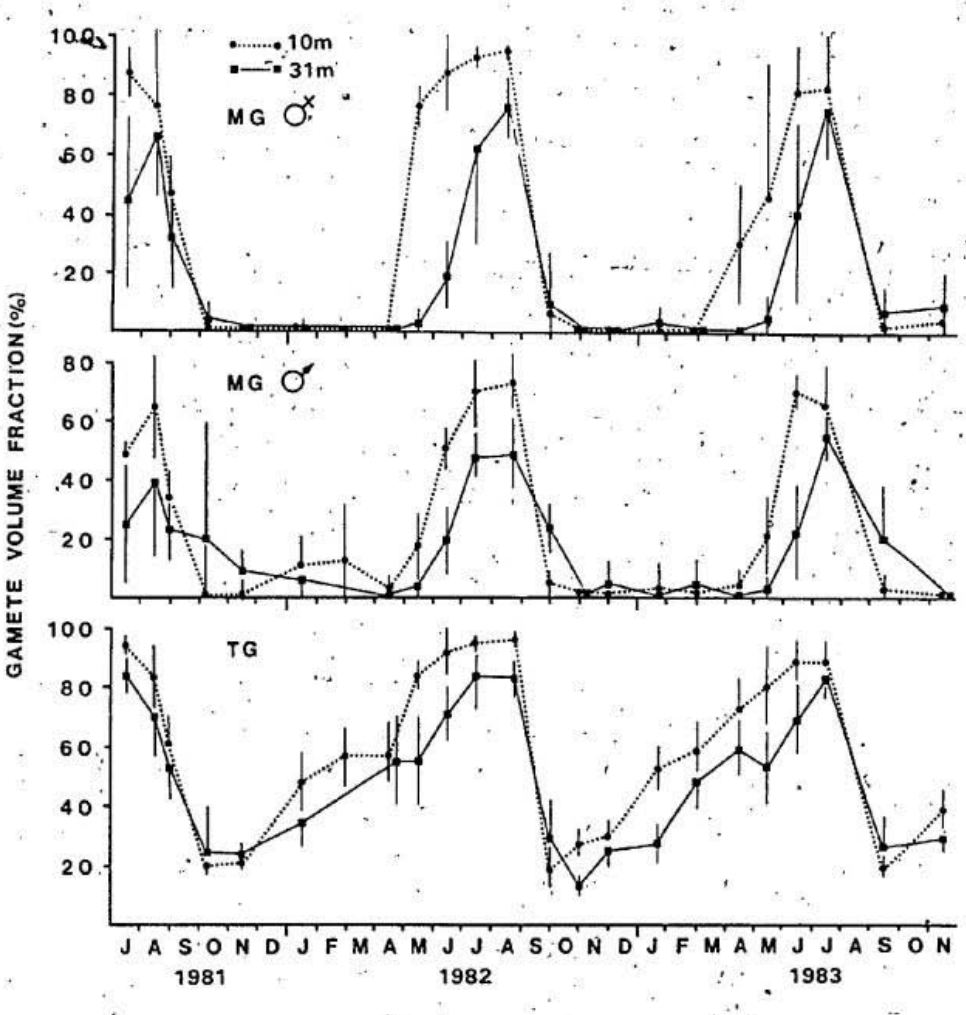


Figure 3-7: Gamete volume fraction for total gametes (TG) in males and females combined, plus mature gametes (MG) for male and female scallops plotted separately. Scallops were collected from 10m and 31m at Sunnyside. The values represent means and 95% confidence intervals.

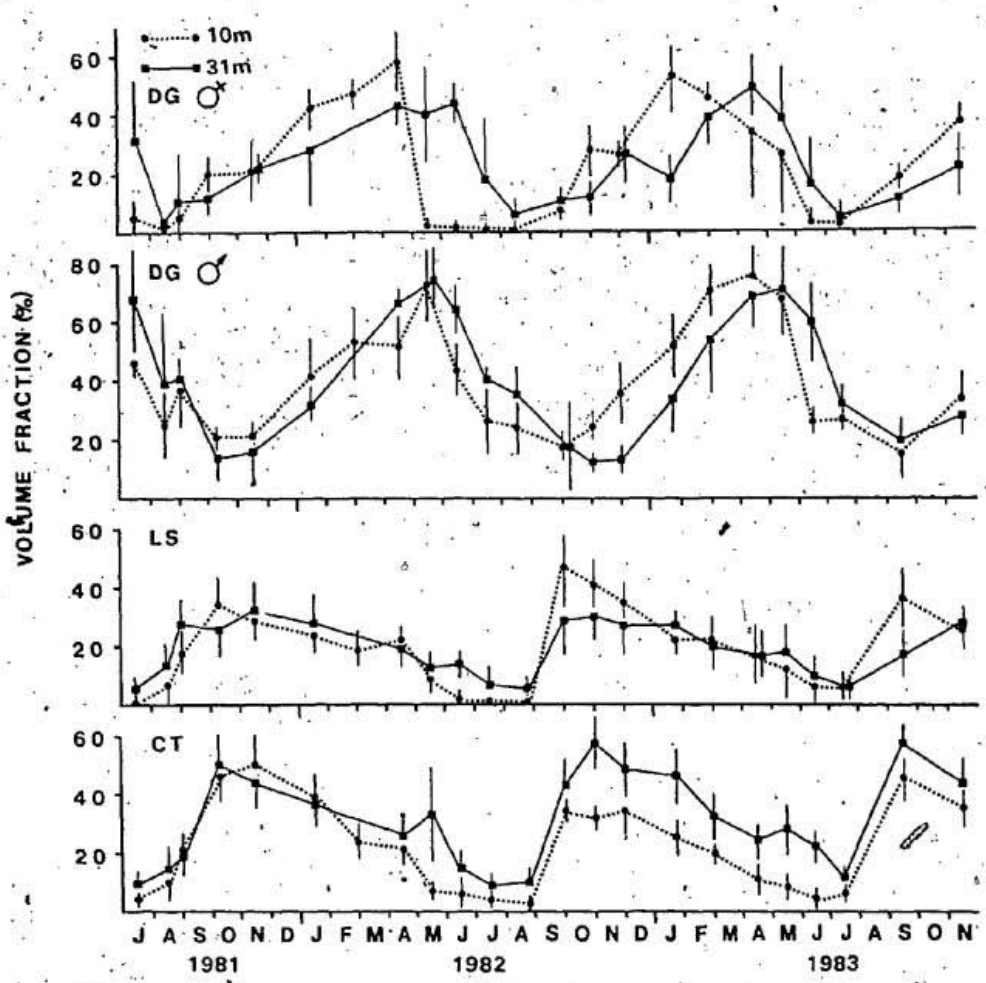


Figure 3-8: Volume fraction of developing gametes (DG), connective tissue (CT) and empty follicle space (LS) for scallops collected from 10m and 31m at Sunnyside. The values represent means and 95% confidence intervals.

significant effects were obtained for interaction terms in addition to the depth and month factors. Single classification analysis of variance performed on data for each month separately indicated that depth was a significant factor for several months of the year:

Treatment	1981			1982			1983		
	F	df	P	F	df	P	F	df	P
Depth	2.4	9,111	.12	28.6	17,196	.001	35.0	15,174	.001
Month	111.8	9,111	.001	105.9	17,196	.001	58.5	15,174	.001
Dep*Mo	1.2	9,111	.31	4.0	17,196	.001	4.05	15,174	.001

The results of a two-way ANOVA indicated that the total GVF was greater for males than females in 1981, 1982 and 1983 for both depths. The interaction term for the 10m population was only significantly different in 1983 and only different in 1982 for the 31m depth population. The effects of month and of sex were highly significant in all comparisons for both populations. By comparing each depth on a monthly basis distinct differences between sexes were observed for several months of the year (ANOVA):

Treatment(10m)	1981			1982			1983		
	F	df	P	F	df	P	F	df	P
Month	111.6	9,50	.001	58.9	19,105	.001	50.3	15,79	.001
Sex	4.2	9,50	.045	3.8	19,105	.05	7.9	15,79	.001
Sex*Mo	1.3	9,50	.28	1.4	19,105	.18	2.3	15,79	.04

Treatment(31m)	1981			1982			1983		
Month	38.3	9,51	.001	64.7	17,84	.001	32.9	15,79	.001
Sex	8.4	9,51	.001	21.4	17,84	.001	37.0	15,79	.001
Sex*Mo	1.3	9,51	.29	2.9	17,84	.006	2.0	15.79	.07

When comparisons were made only on months with peak GVF in 1981-1983, there were no differences between the 10m and 31m scallops, or between males and females for each depth:

	1981			1982			1983		
	F	df	P	F	df	P	F	df	P
Males vs (10m) Females (31m)	1.0	1,11	.33	0.1	1,19	.93	1.2	1,11	.29
	0.1	1,11	.86	0.2	1,19	.65	1.5	1,11	.25
10m vs 31m	2.1	1,23	.16	1.3	1,39	.26	1.1	1,23	.30

3.2.2. Egg Diameter

There was no difference between estimates of oocyte diameter using histological sections or using the Coulter counter technique. The means and 95% confidence intervals were 68.8 $\pm 5.2\mu m$ and 69.1$\pm$1.1μm for each method respectively (1983 data). More variation in diameter was observed in the histological sections where the oocytes were closely packed and often appeared irregular or polygonal in shape. There was very little variation in mean diameter of the eggs actually spawned by the females and sized by the Coulter counter, which may be attributable to the fact that the mature oocytes become rounded on contact with the water (Naidu,1970).

Egg diameter determined with the Coulter counter was significantly greater in 1982 than 1983 but there was no difference between depths in either year. Mean egg diameters for the 10m population in 1982 and 1983 were 71.2 μm ($\pm$3.0) and 68.5 μm ($\pm$1.1) and the values for the 31m population were 71.6 μm ($\pm$1.6) and 70.0 μm ($\pm$3.1):

Treatment	F	df	P
Depth	2.1	3,16	.17
Year	10.7	3,16	.005
Depth*year	0.7	3,16	.41

Although the overall difference in the average linear dimensions between 1982 and

1983 was less than 4% the corresponding difference in volume was approximately 10%.

3.3. Physiological Measurements

Oxygen consumption and clearance rates measured during July, September and November for complete size ranges of scallops from Sunnyside were compared using multiple regression analysis (ANCOVA). When using the Bonferroni approximation for three-way regression comparisons a more conservative significance level of 0.05/3 (α=.05) or approximately 0.016 is desirable before rejecting the null hypothesis. A summary of t values, degrees of freedom and test significances for slope and intercept comparisons of oxygen consumption and clearance rates related to total body weight for the months July, September and November is presented in Table 3-1. A summary of the parameters and statistics for these equations are presented in Table A-1.

None of the slopes for metabolic or clearance rates were significantly different at the 0.016 level, but intercepts were often significantly different. Rates of O_2 consumption were similar in July and September but significantly higher than November, whereas clearance rates were at their maximum in September and greater than the similar rates seen in July and November. These trends applied to both depths.

A method described by Sokal and Rohlf (1981) was used to calculate common slopes of 0.69 and 0.88 (10m) and 0.71 and 0.89 (31m) for clearance rate and oxygen consumption respectively. The results of an overall comparison (ANCOVA) of these rates for July, September and November combined revealed no differences in clearance rates (slope t=0.80, df=3,115, P<.43, intercept t=1.03, df=3,115, P<.31) between water depths with only the intercepts for oxygen consumption rates being different (slope t=0.54, df=3,115, P<.59, intercept t=4.88, df=3,115, P<.001). Common values for both depths of 0.70 for the slope of clearance rates and 0.89 for oxygen consumption rates were

Table 3-1: A summary of t values for comparisons of clearance and oxygen consumption rates calculated in different months for scallops from 10m and 31m at Sunnyside. Significant differences in this table and all subsequent tables are indicated by asterisks (*P<.05,**P<.01,***P<.001). Note that for a three way comparison one asterisk indicates a significance level between 0.01 and 0.016.

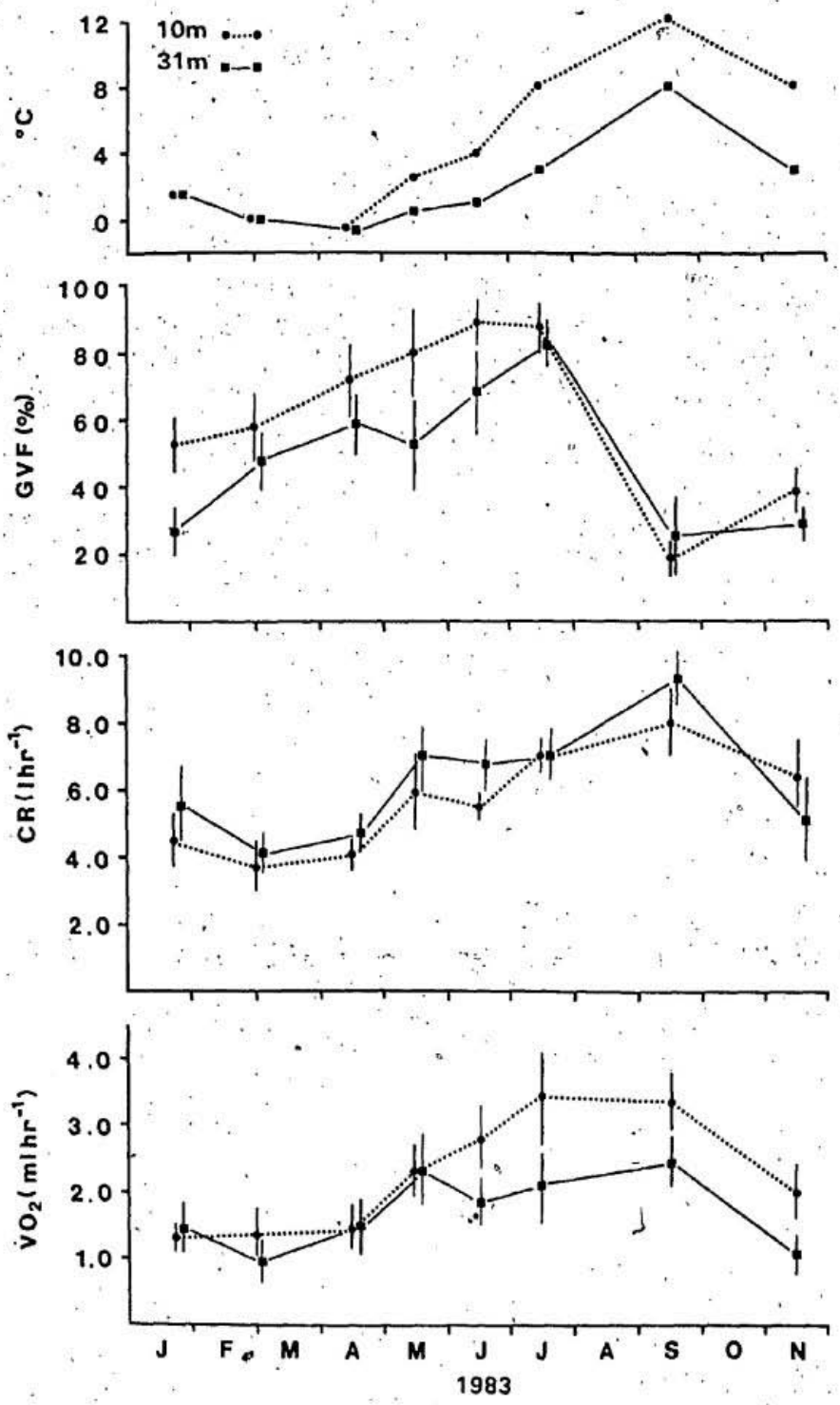
10m df=5,55	Slopes		Elevations	
	CR	O_2	CR	O_2
July and Sept	2.06	1.06	3.66***	0.60
July and Nov	1.39	2.38	0.76	10.06***
Sept and Nov	0.80	1.31	2.75**	8.76***

31m df=5,52	Slopes		Elevations	
	CR	O_2	CR	O_2
July and Sept	0.21	0.30	3.43***	2.01
July and Nov	0.04	1.88	2.16	8.88***
Sept and Nov	0.19	1.44	5.81***	11.33***

therefore used to obtain standardized rates for a scallop having a total weight of 20g (Figure 3-9).

Metabolic rates were low and approximately equal in both the 10m and 31m populations between January and May but much greater rates were evident between June and November when the water was warmer, especially for the shallow population (Figure 3-9). Seasonal changes in clearance rates were not as pronounced but the lowest rates for both populations were generally observed during the winter months. There were highly significant differences in these standardized rates between depths and between months (two way ANOVA).

Figure 3-9: Mean standardized oxygen consumption and clearance rates plus 95% confidence intervals for 20 g scallops from 10m and 31m at Sunnyside. Values for GVF and ambient temperatures during the study are also included.


10m
31m
°C
12
8
4
0
GVF (%)
100
80
60
40
20
CR (l hr⁻¹)
10.0
8.0
6.0
4.0
2.0
VO₂ (ml hr⁻¹)
4.0
3.0
2.0
1.0
J
F
M
A
M
J
J
A
S
O
N
1983

	Clearance			VO_2		
Treatment	F	df	P	F	df	P
Month	42.1	15,113	.001	33.8	15,113	.001
Dep	11.2	15,113	.001	40.6	15,113	.001
Mo*Dep	3.2	15,113	.004	5.5	15,113	.001

Comparisons of clearance rates between depths for each month sampled revealed that clearance rates were only different in April, June and September:

Clearance	April			June			September		
	F	df	P	F	df	P	F	df	P
10m vs 31m	4.5	1,14	.05	24.2	1,14	.001	6.5	1,17	.02

Similarities in oxygen consumption rates between depths were observed for the months from January to May, but higher metabolic rates were recorded for the 10m samples in June , July, September and November:

Metabolic Rate	June			July		
	F	df	P	F	df	P
10m vs 31m	18.4	1,14	.001	15.1	1,15	.002
	September			November		
	16.2	1,17	.001	21.7	1,13	.001

3.4. Population Structure

3.4.1. Density, Size Frequency Distribution and Biomass

A total of 96 scallops of various sizes was counted in the Sunnyside grid enclosing an area of approximately 512 m^2. Density ranged from zero to eight individuals per 16 m^2 section, giving a mean of 0.19±.04 scallops m^{-2}. The Colinet grid covered an area of 384 m^2 and contained 324 scallops. A range of 5 to 21 scallops per 16 m^2 section was found with a mean density of 0.84±.11 individuals per square metre. These values for *Placopecten magellanicus* were much less than density estimates of 4.0 and 2.3 m^{-2} recorded by Naidu (1969) for commercial beds off the west coast of Newfoundland. In exploratory studies by Wilton (1981) much lower values (<0.20 m^{-2}) were observed for another area off the coast of western Newfoundland. A range of 0.1-4.8 individuals m^{-2} for the Northumberland Strait was reported by Caddy (1970), whereas spat may reach numbers of up to 123 m^{-2} on the Georges Bank (Larsen and Lee,1978). According to Vahl (1982) densities of adult *Chlamys islandica*, a smaller species of scallop than *P. magellanicus*, may attain 75 m^{-2} in northern Norway.

The majority of the scallops in Sunnyside belonged to the larger size classes (>14 cm) with modes at 12-13 cm and 16-17 cm (Figure 3-10). Few individuals were less than 10 cm in shell height. A more uniform distribution was observed for the Colinet population where the small size classes were better represented and modes were observed at 9-10 cm and 13-14 cm. Size frequency distributions similar to that for Sunnyside, in which the majority of individuals are in the moderately large size classes with few representatives in the smaller classes, have been presented for *Placopecten magellanicus* by Caddy et al. (1970), D'Amours and Pilote (1982) and Jamieson et al. (1981a).

Despite a density four times greater in Colinet than in Sunnyside the biomass (g m^{-2}) was only two and a half times greater in the former and the export of gametes (g $m^{-2}yr^{-1}$) was only one and a half times more. This is

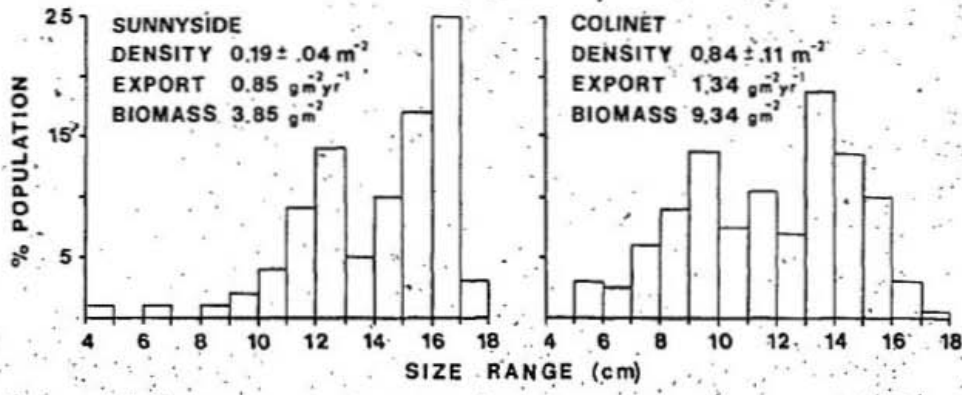


Figure 3-10: Size frequency distributions for populations of scallops from Sunnyside and Colinet.

probably partially due to the greater proportions of larger scallops and greater size specific fecundities and somatic growth rates in the Sunnyside population (see section 3.6.2).

3.4.2. Mortality

Ten different sized scallops with known heights were placed on the bottom in Colinet and photographed. The mean error in assigning a height to a scallop shell in a photograph was approximately +3.5±2.6%. Initial numbers in each size group were estimated from photographs taken at the beginning of the study. The number of scallops in any given size class that died during the 18 month study, plus the mortality rates, are given in Table 3-2 and the percent mortality values plotted in Figure 3-11. The line drawn through the points represents the quadratic polynomial fitted to the data. The regression equation was $y=0.0079+.0005(x-\bar{x})+.0000105(x-\bar{x})^2$ where $\bar{x}=11.0$ cm ($F=8.21$, $df=12$, $P=.009$, $r^2=0.65$). Age specific mortality and survivorship values were derived

Table 3-2: Estimates of age specific mortality rates for scallops observed for 18 months in the Colinet grid.

Size Class(cm)	#Initially Alive	#Dead(1.5yr)	Mortality(yr)
5-6	9	7	0.52
6-7	8	1	0.08
7-8	19	1	0.04
8-9	30	6	0.13
9-10	41	3	0.05
10-11	24	2	0.06
11-12	34	0	0.00
12-13	23	1	0.03
13-14	57	5	0.06
14-15	43	11	0.17
15-16	32	6	0.13
16-17	9	4	0.30
17-18	2	0	0.00

Annual Rate =(47/330 x 100)/1.5yr=9.5%

from these data. Mortality rates were high during the first few years but declined to very low values at six to eight years of age (11-13 cm) and then gradually increased, resulting in a U-shaped curve. A similar mortality curve was described by Thompson (1984a) for *Mytilus edulis* in eastern Newfoundland.

An overall annual mortality rate of 9.5% was estimated for all sizes sampled which was very similar to previous estimates of 10% (Dickie,1955; Merrill and Posgay, 1964) for the same species obtained by determining the proportion of *cluckers* in a dredged sample. The estimate of 9.5% was higher than the 6.9% recorded by D'Amours and Pilote (1982) and very much greater than the series of values (1-9.2%) from studies in the Gulf of St. Lawrence summarized by D'Amours and Pilote (1982).

Mortality estimates for other species of scallops include 17% for *Chlamys*

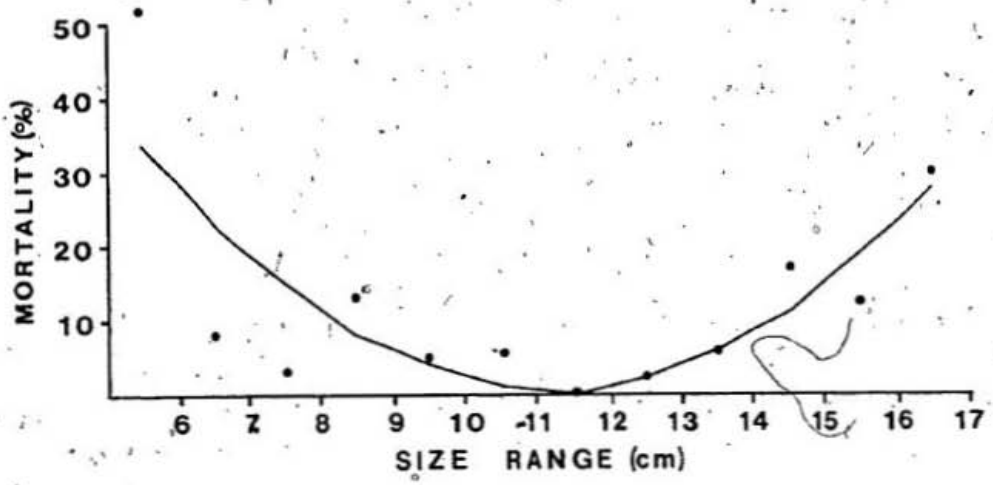


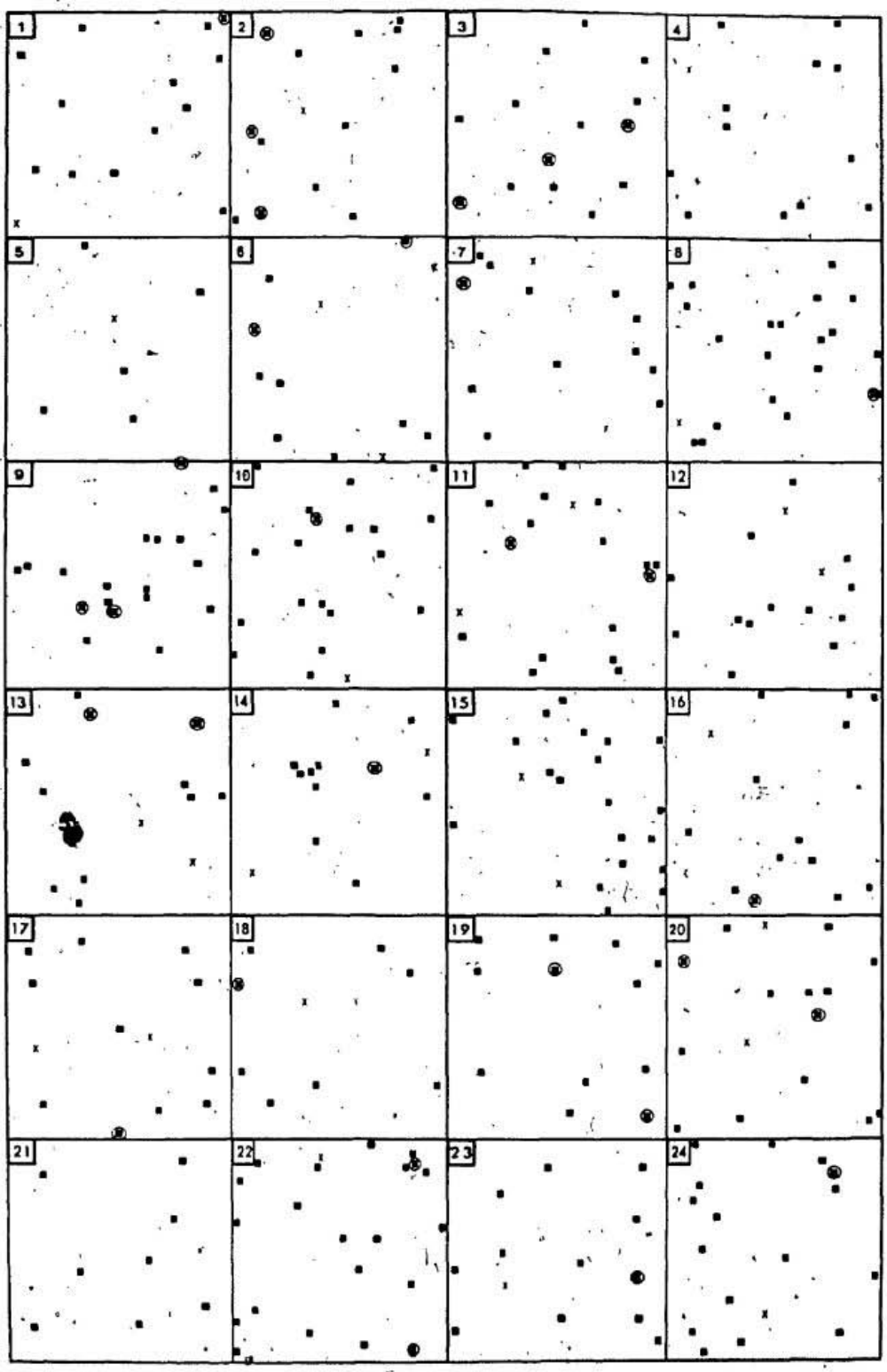
Figure 3-11: Mortality curve fitted by a polynomial equation.

islandica (Vahl,1981a), 26% for *Pecten maximus* (Baird,1966), an age specific range of 15 - 68% (Gruffydd,1974a) for unfished populations of *P. maximus* and of 10-56% for a commercial bed of *P. maximus* (Gruffydd,1972).

3.4.3. Spatial Distribution Pattern

The spatial arrangement and positions of random points and scallops used to perform Hopkins and Skellam's (1954) test for randomness in the Colinet scallop population are seen in Figure 3-12. The value obtained for the test statistic was greater than one, indicating that the scallops were aggregated.

Figure 3-12: Positions of scallops (squares) in the Colinet grid. Crosses represent 30 points and squares enclosed in circles represent the 30 randomly located scallops used to test for randomness.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3.5. Comparisons of Methods for Determining Age

3.5.1. Estimates of Accuracy Using Specimens of Known Age

In any series of age estimates two types of error are possible. The first is accuracy, whereby variation from the true age (rather than an assigned or average age) is considered, and the second is precision, representing the variation associated with several estimates for any given sample, usually without consideration of the true (unknown?) age. In a test using only cultured scallops of known age the variation from true age (accuracy) and the consistency with which ages were assigned (precision) was obtained simultaneously for four observers using two methods (ligament,external rings on the shell).

A two way ANOVA revealed a significant interaction term ($F=3.84$, $df=7,72$, $P<.013$) between observer and method, indicating that one method could be better than the other depending on which observer was using it, but a one way ANOVA with method as the treatment and considering all the observers demonstrated that the ligament method ($\bar{x}=15.8$) produced significantly less error than the external ring method ($\bar{x}=27.9$) ($F=10.35$, $df=1,78$, $P< .002$). Additional one way ANOVAs demonstrated a difference between observers for the ligament method ($F=3.77$, $df=3,36$, $P<.02$) and for the external method ($F=3.11$, $df=3,36$, $P<.04$). For example, using the ligament method observer #4 had an average total error of only 4.8% whereas observer #2 had an average of 24.4%. When the external ring method was employed, however,observer #3 was best with 14.8% error while observer #1 had an average total error of 34.9%.

In this study a total of 240 age estimates were considered (4 observers x 2 methods x 3 trials x 10 scallops) of which 101 were exactly correct with 117 overestimates and 22 underestimates i.e. a five times greater chance of overestimating than underestimating in the 60% of cases where age was not determined correctly. The problem of overestimating the ages of young specimens and underestimating those of old ones from external growth lines in *Spisula*

solidissima has been discussed by Jones et al. (1978),and it is probably a common difficulty in determining age in most bivalve species.

3.5.2. Precision Estimates for All Test Specimens

The interaction term for observer by method for the variation in repeated estimates from a mean estimate (precision) demonstrated a significant effect. The method factor was significant while the observer factor was not. Three separate one way ANOVA's demonstrated that the ligament method gave more reproducible results than the external ring method for all observers combined ($F=5.00$, $df=1,238$, $P<.03$), but none of the observers were significantly better than the others using either method (ligament $F=1.83$, $df=3,116$, $P<.15$; shell annuli $F=1.75$, $df=3,116$, $P<.16$).

Treatment	F	df	P
Method	5.1	7,232	.03
Observer	0.2	7,232	.88
Meth*Obs	3.3	7,232	.02

The results of these two age studies indicate that neither method is ideal, but that the increments on the ligament more accurately reveal the true age and give more consistent results than counting external annuli on the shell. These observations are based on the assumption that both external and ligament growth increments are consistently formed in an annual pattern. Johannessen (1973) concluded that external rings could only be used with certainty for a few specimens of *Chlamys islandica* and that the ligament method was superior. No differences existed here between observers in how consistently they assign ages to specimens, but a more powerful test considering accuracy and precision revealed that some observers were better than others depending on the methodology. High variability between observers has also been demonstrated in counting growth lines in two other bivalve species (Crabtree et al., 1980).

In studies specifically involving *Placopecten magellanicus* Hidu et al. (1977) expressed a lack of confidence in the ligament method based on poor correspondence between two independent observers, but considered the external rings to be even more difficult to interpret. Merrill et al. (1966) found good correspondence between two observers in the recognition of external annuli, so the usefulness of these methods for age determination in *P. magellanicus* may vary with the locality of collection, the researcher's definition of acceptable correspondence or the experience of the observers, although experts in determining age for fish have been known to disagree significantly on identical specimens (Lopez-Veigna et al., 1977).

3.6. Somatic and Shell Growth Rates

The Von Bertalanffy growth function has been used to describe growth characteristics for a variety of organisms. Rafail (1972) used a simple modified parabola (polynomial) to describe growth for several species of fish . The major advantages of this method over the Von Bertalanffy function include the opportunity to test differences mathematically, since , unlike the latter , it can be used for linear comparisons, and if an asymptote is not observed in the data there is no attempt to force asymptotic behaviour (Roff,1980).

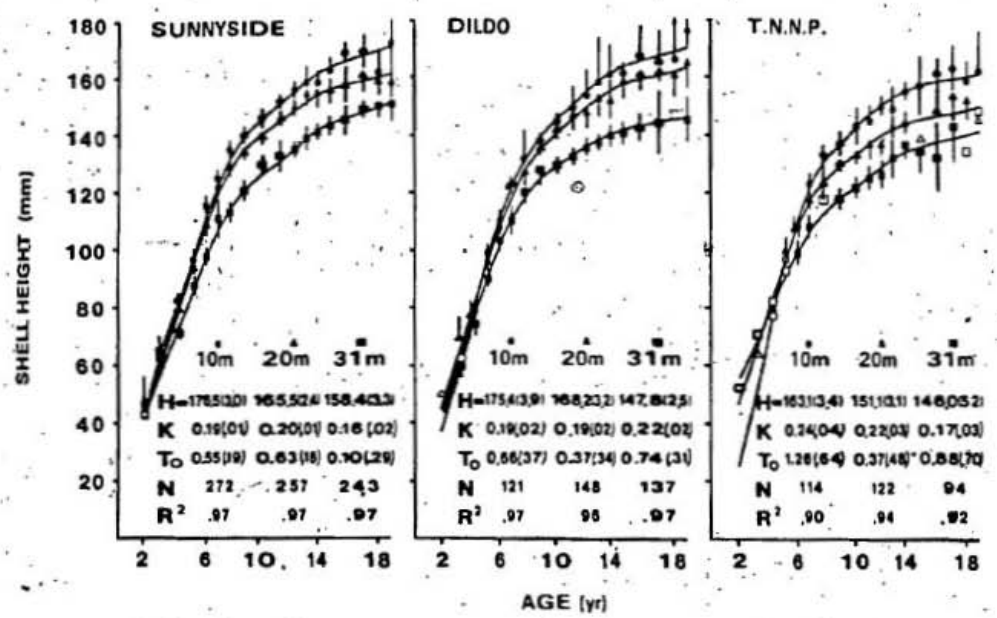
For the purposes of comparing the growth curves observed in this study and for comparisons with published growth curves both polynomials and Von Bertalanffy equations were fitted to the shell growth data. Only polynomials were fitted to the somatic weight data. In order to evaluate the possible effects of water depth for example, it was necessary to keep the other two variables constant by comparing samples collected from identical locations in the same year. When no differences in growth rates or body component weights per unit shell height were observed then common equations were used to describe the relationships. Combining yearly estimates for identical sites and depths was the most frequent occurrence probably due to the fact that the same population was sampled on successive dates.

The means and their 95% confidence intervals for shell heights and somatic weights of each age class from different water depths in Sunnyside, Dildo and Terra Nova National Park are presented in Figure 3-13. Similar data for populations from Colinet, Spencers Cove , Southern Harbour, New Jersey and St. Andrews are provided in Figure 3-14. The lines drawn through the shell height data represent the values predicted from a Von Bertalanffy equation. The 95% confidence intervals for the parameters are presented in brackets , sample size and values for r^2 were also included in the figures. The lines fitted to the somatic weight data represent values obtained from the polynomial equation with the parameters, sample size and values for r^2 also included in the figures.

Predicted values for heights in each age class obtained from Von Bertalanffy and polynomial equations for Sunnyside scallops were compared (Table 3-3). The series of values are almost identical and after age three vary less than 3.5 mm (or 2%) in height. This agrees with previous findings of Rafail (1972) that a polynomial presents an equivalent or better fit than a Von Bertalanffy equation. The relatively narrow confidence intervals and high r^2 values indicated that both equations adequately described the growth of scallops from several locations. The close agreement between the estimates obtained with the less well known method of polynomial regression and the more common Von Bertalanffy technique added credence to the statistical comparison of population samples using polynomial regression. Gompertz growth equations were also fitted to the data but unrealistically low estimates of asymptotic sizes were obtained, perhaps because of the absence of one year old scallops from the samples. More satisfactory results have also been obtained with the Von Bertalanffy than Gompertz equations in *Macoma balthica* (Bachelet,1980), *Choromytilus meridionalis* (Griffiths,1981a) and *Mytilus galloprovincialis* (Ceccherelli and Rossi,1984), although Bayne and Worrall (1980) reached the opposite conclusion in their study of *Mytilus edulis*.

The variability of somatic weight in a given age class was greater than shell height as indicated by the larger confidence intervals and lower r^2 values (Figures

Figure 3-13: Age specific shell heights fitted to Von Bertalanffy equations and somatic weights fitted to polynomials for scallop populations from Sunnyside, Dildo and TNNP. Solid symbols represent mean heights or weights plus 95% confidence intervals for age classes consisting of more than three individuals, whereas open symbols represent means only for age classes consisting of less-than three individuals.


SUNNYSIDE
DILDO
T.N.N.P.
SHELL HEIGHT (mm)
AGE (yr)
10m 20m 31m
H= 176.5(3.0) 165.5(2.4) 158.4(3.3)
K 0.19(.01) 0.20(.01) 0.16 (.02)
To 0.55(.19) 0.63(.18) 0.10(.29)
N 272 257 243
R² .97 .97 .97
H=175.4(3.9) 168.2(3.2) 147.8(2.5)
K 0.19(.02) 0.19(.02) 0.22(.02)
To 0.66(.37) 0.37(.34) 0.74 (.31)
N 121 148 137
R² .97 .96 .97
H=163.1(3.4) 151.1(3.1) 146.0(5.2)
K 0.24(.04) 0.22(.03) 0.17(.03)
To 1.26(.64) 0.37(.48) 0.88(.70)
N 114 122 94
R² .90 .94 .92

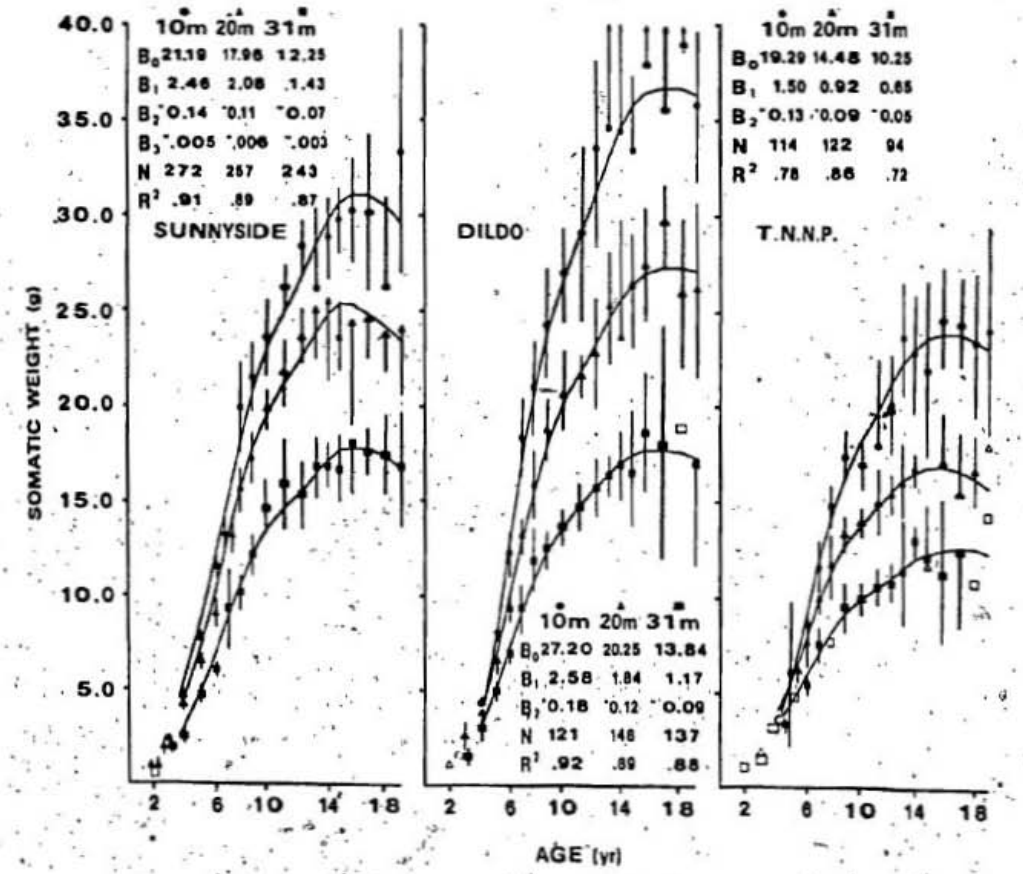
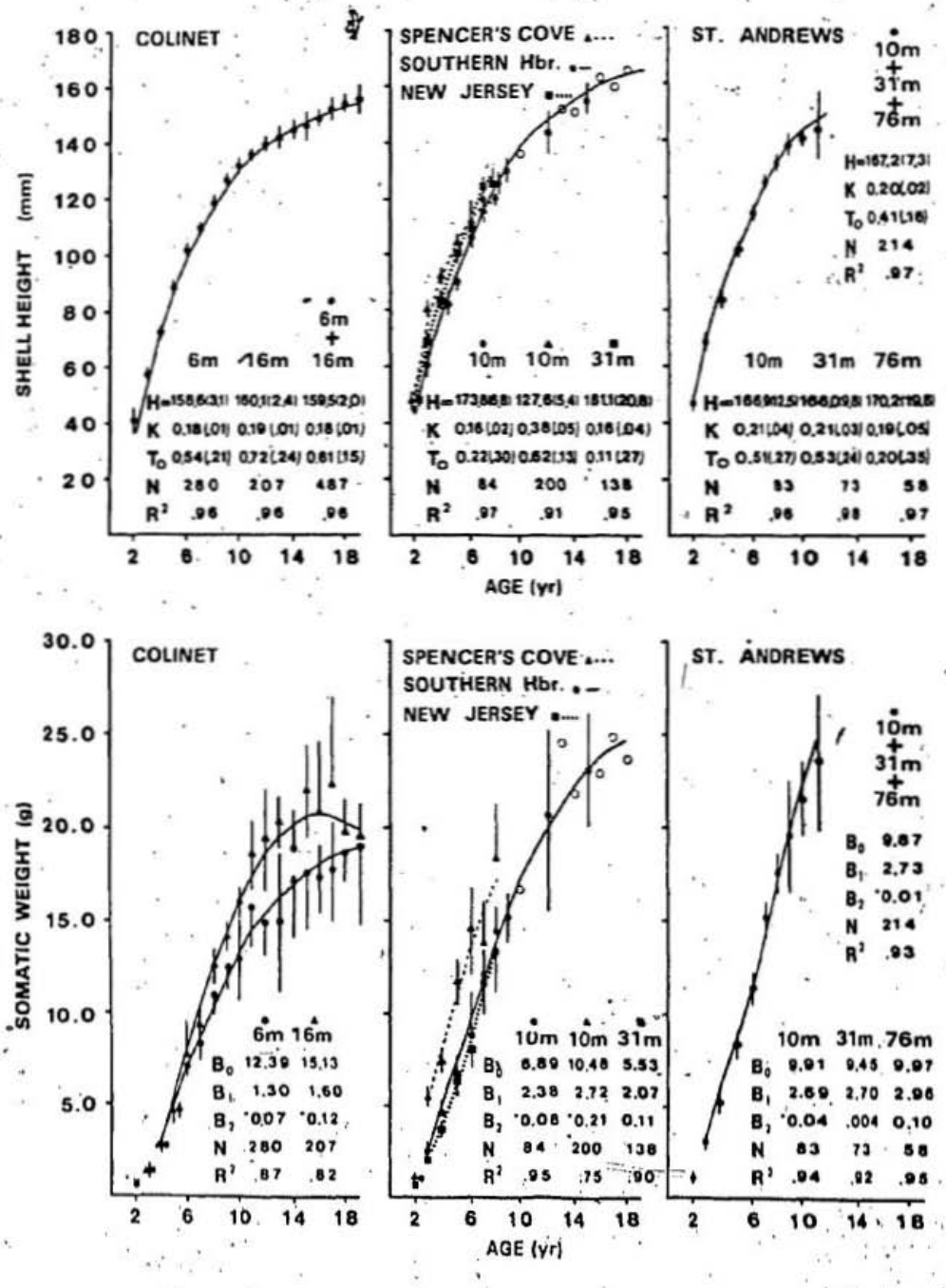

SOMATIC WEIGHT (g)
AGE (yr)
10m 20m 31m
B0 21.19 17.96 12.25
B1 2.46 2.08 1.43
B2 -0.14 -0.11 -0.07
B3 -.005 -.006 -.003
N 272 257 243
R² .91 .89 .87
SUNNYSIDE
B0 27.20 20.25 13.84
B1 2.58 1.84 1.17
B2 -0.18 -0.12 -0.09
N 121 148 137
R² .92 .89 .88
DILDO
B0 19.29 14.48 10.25
B1 1.50 0.92 0.65
B2 -0.13 -0.09 -0.05
N 114 122 94
R² .78 .86 .72
T.N.N.P.

Table 3-3: Comparisons of shell heights obtained using the Von Bertalanffy equation and polynomial regression for scallops collected from 10m, 20m and 31m at Sunnyside.

	10m		20m		31m	
AGE	VB	PR	VB	PR	VB	PR
2	41.4	43.3	39.7	43.4	41.9	43.1
3	64.2	64.2	62.6	63.3	59.3	59.5
4	83.2	82.4	81.4	80.6	74.2	73.9
5	99.0	98.2	96.7	95.6	86.8	86.6
6	112.1	111.6	109.2	108.5	97.5	97.5
7	122.9	122.9	119.5	119.4	106.6	106.9
8	132.0	132.4	127.8	128.5	114.3	114.9
9	139.5	140.2	134.7	136.0	120.9	121.6
10	145.8	146.4	140.3	142.1	126.5	127.2
11	150.9	151.4	144.9	146.9	131.3	131.8
12	155.3	155.2	148.6	150.7	135.4	135.6
13	158.8	158.2	151.7	153.6	138.8	138.8
14	161.8	160.5	154.2	155.7	141.7	141.4
15	164.3	162.2	156.3	157.4	144.2	143.6
16	166.4	163.7	158.0	158.7	146.3	145.5
17	168.1	165.0	159.3	159.8	148.1	147.3
18	169.5	166.4	160.5	160.9	149.7	149.2
19	170.7	168.1	161.4	162.3	151.0	151.3

Figure 3-14: Age specific shell heights fitted to Von Bertalanffy equations and somatic weights fitted to polynomials for scallop populations at Colinet, Southern Harbour, Spencers Cove, New Jersey, and St.Andrews. Solid symbols represent mean heights or weights plus 95% confidence intervals for age classes consisting of more than three individuals, whereas open symbols represent means only for age classes consisting of less than three individuals.


COLINET
SPENCER'S COVE
SOUTHERN Hbr.
NEW JERSEY
ST. ANDREWS
SHELL HEIGHT (mm)
AGE (yr)
SOMATIC WEIGHT (g)
6m
16m
31m
76m

3-13,3-14). In comparison with the forced asymptotic fit of the Von Bertalanffy function, the less restrictive polynomial equation was especially advantageous in describing the relationship between somatic weight and age. For example, in Figures 3-13 and 3-14, 12 of the 14 populations containing scallops greater than 12 years of age displayed a general decline in weight after approximately 16-17 years. The two exceptions were Colinet (6m) and Southern Harbour (10m). However, only a few scallops (<12) were found in the last six age classes from Southern Harbour making interpretation difficult.

3.6.1. Depth Related Differences

With the exception of the first three or four years of growth the mean shell height for each age class was consistently lower in those scallop samples collected from greater water depths at Sunnyside, Dildo and TNNP (Figure 3-13). The same trend was seen in asymptotic shell heights, whereas the k values (representing the relative rate at which the animals in the samples reached their asymptotic sizes) were very similar between depths. For example, whereas the scallops from 10m reached a greater maximum size than those from 31m, both groups apparently reached their maximum sizes at the same rate. The greatest difference between depths was seen in the 10m and 31m samples with the 20m sample usually exhibiting intermediate values. Exceptions to this trend were seen at Colinet and St. Andrews where both k and H_∞ values were independent of depth (Figure 3-14).

Due to the great number of regression equations and statistical comparisons in the next three sections, the data have been presented in Appendix (Tables A-2 to A-29). The parameters and statistics for the cubic polynomials fitted to shell heights are given in Table A-2. The results of several multiple comparisons among depths, using cubic polynomial equations fitted to shell heights and Von Bertalanffy equations , are summarized in Tables A-3,A-4. In general, the statistical analyses confirm the conclusions reached in comparing Von Bertalanffy curves, i.e. slower shell growth in scallops from deeper water. Samples from each

depth were significantly different from one another for at least the β_0 parameter in the polynomial comparisons, and usually at least for the H∞ estimate in the Von Bertalanffy comparisons. The k values were not significantly different between any 10m and 20m populations or for any of the Dildo samples. Again, no differences in shell growth between scallops from different water depths were observed in the St. Andrews data. The earlier conclusion that there were no differences between the Colinet samples was confirmed by the Von Bertalanffy comparison but not by the polynomial comparison, which demonstrated a difference between depths. This was the only occasion on which there was a discrepancy between the two methods of comparing growth curves. The Von Bertalanffy comparison has advantages over the polynomial comparison in that it has been widely used and its parameters have biological meaning.

Depth related differences in shell growth may also be demonstrated by comparing simple linear relationships between shell weight and shell height (both variates log transformed). This dependent variable gives an indication of shell thickness for scallops of comparable size. All possible depth combinations revealed significant differences (Table A-5). Similarities among slopes and differences in intercepts were observed, with three exceptions: Colinet (6m,16m), Dildo (20m,31m) and TNNP (10m,20m) where different slopes were obtained. Heavier shells were generally found in scallops from shallower water. The scallops collected from 10m and 76m in St. Andrews were similar but both differed from the 31m sample in the relationship between shell weight and shell height.

For reasons previously mentioned the relationships between somatic weight and age were only described using polynomial regression (Figure 3-13, 3-14). Like the curves describing shell height, the somatic growth curves diverge after the first few years, except at St. Andrews, where there were no obvious differences between the equations for each depth (Figure 3-14). The heaviest scallops in each age class were collected from shallower water except at Colinet, where the reverse trend was observed. Differences in somatic weight between depths were more

pronounced than differences in shell height. For example, at Dildo, where the maximum mean weight of 17 year old scallops was 17.7 g in the 31m sample and 36.3 g in the 10m sample (a difference of 52%), the corresponding heights (10m=167.0 mm and 31m=143.8 mm) only differed by 14% (Figure 3-13).

The results of several multiple depth comparisons among cubic and quadratic polynomial equations fitted to somatic weight and age data are summarized in Table A-6. The $\bar{x}$ values used in the equations are as follows Sunnyside 9.41; Dildo 10.24; TNNP 10.76; Colinet 9.51; Spencers Cove, Southern Harbour and New Jersey 4.82; and St. Andrews 5.44. These analyses demonstrate differences in somatic weight versus age relationships between samples collected from different water depths at any given site. In most cases significant differences were seen between all parameters of the equations with the exception of the St. Andrews data, where again no depth related differences were observed.

The final approach to comparing the somatic weights of scallops from various depths was to determine whether there were differences in the simple linear equations relating somatic weight to shell height (both variates log transformed). This method corrects for previously described differences between sizes at given age for scallops from different depths so that the weights of scallops of equal heights may be compared regardless of their respective ages. The results of these comparisons for 1981 and 1982 have been in Table A-7 and the 1983 comparisons presented in Table A-8. With the exception of the regressions for Colinet samples, which possessed different slopes, all the inter-depth comparisons for Sunnyside and Dildo displayed similar slopes but different intercepts in 1981 (Table A-7). Differences in elevation but not in slope between depths were demonstrated for Dildo, TNNP and Colinet in 1982, but at Sunnyside the slope for the 31m sample was different from the other two samples (10m, 20m), which were identical. In 1983, the shallowest and deepest collections from Sunnyside displayed different slopes (Table A-8), whereas similar slopes but different intercepts were seen for the other combinations, but at Dildo the 10m and 20m

samples had similar equations, but both differed in elevation from the 31m sample. On the other hand, in 1983 similar equations in Terra Nova were obtained for the 20m and 31m collections, both of them differing in intercept from the 10m sample. In 1983 no significant differences were demonstrated between the Colinet samples or between scallops from 10m and 31m at St. Andrews. However, both the 10m and 31m samples from St. Andrews differed in intercept from those scallops collected in 76m.

With the exception of one pair of comparisons the somatic weights for the various samples differed from one another on every occasion. This again demonstrates that body weight is consistently greater in scallops from shallower water (excepting Colinet) than in those from deeper water .

3.6.2. Site Related Differences

Von Bertalanffy curves for shell growth of scallops from equivalent water depths at different collection sites in Newfoundland were compared (Figure 3-13). H_∞ and k values for 10m and 20m were identical for the Sunnyside and Dildo samples, and the Southern Harbour value was similar to the 10m values from both these sites. For 31m, however, the Sunnyside H_∞ value was higher and the k value was lower than the corresponding Dildo values.

The TNNP collections from 10m and 20m depth had much lower H_∞ values but slightly higher k values than comparable samples from Sunnyside and Dildo. The scallops from 31m had a much lower H_∞ value and an approximately equal k compared with Sunnyside scallops, but a similar H_∞ value and a lower k value than Dildo scallops.

Scallops from Colinet may be compared with those from other sites if one assumes that a depth of 6m in Colinet is approximately equivalent to 10m elsewhere, and 16m equivalent to 20m. The maximum height of a Colinet scallop from 6m was less than that of a shallow water scallop at any other site, but the k

value was the same. Similar results were obtained from comparisons of scallops from 16m at Colinet with those from corresponding depths at Sunnyside and Dildo, although the growth coefficient k was slightly lower than at TNNP.

The results of three-way polynomial and Von Bertalanffy comparisons of shell height and age relationships are presented in Tables A-9,A-10. There were no significant differences between scallops from 10m and 20m at Sunnyside or Dildo, but considerable differences were seen between 31m samples at these sites. The conclusions reached from the polynomial comparisons were similar to those based on the results of the Von Bertalanffy comparisons, except that there were no differences between the 10m samples from Dildo and TNNP. The comparison of Von Bertalanffy curves, however, indicated that there were considerable differences between these populations in both the H_∞ and k values. For this one example, fitting the Von Bertalanffy and the polynomial equations to the same data resulted in different conclusions. In general scallops from Sunnyside and Dildo were growing at similar rates but faster than those from TNNP or Colinet.

With the exception of the age specific somatic weights from the 10m samples, (higher in the Dildo population) scallops from 20m and 31m at Dildo and Sunnyside were similar (Figure 3-13). However, scallop somatic weights for corresponding depths in TNNP, Colinet and Southern Harbour were generally lower than those from Sunnyside or Dildo. The lowest values were seen in scallops from 31m in TNNP.

Comparisons of polynomial equations for somatic weight versus age data were complicated by the fact that the Sunnyside populations had significant cubic coefficients whereas only quadratic terms were significant in the other samples compared. This may indicate that Sunnyside was substantially different from other sites or it may be partially attributable to the greater sample sizes, resulting in an improved polynomial fit. Sample size may not have been as critical in fitting polynomials to the shell height data because heights were much more conservative with age than weight and a larger sample size would not have

improved the fit. In the interests of simplification, the Sunnyside somatic weight data were therefore fitted to quadratic rather than cubic polynomials, so that direct comparisons could be made with other sites. The quadratics for the Sunnyside weight data are as follows:

Dep(m)	β_0	β_1	β_2	n	r^2
10	21.36	2.27	-0.14	272	0.91
20	18.18	1.84	-0.13	257	0.89
31	12.55	1.31	-0.09	243	0.87

Somatic weights for TNNP scallops were significantly different at all depths from those of Sunnyside and Dildo scallops (Table A-11), and animals from 10m at Dildo were heavier than those from 10m at Sunnyside. Samples from 20m in Sunnyside were different from those in Dildo, but at 31m somatic growth rates were equal. Overall, Sunnyside and Dildo scallops not only had greater shell growth rates than the other scallops but greater somatic growth rates as well.

The results of several comparisons between sites in each year for somatic weight versus shell height (both variates log transformed) at identical depths in Sunnyside, Dildo and TNNP are presented in Table A-12. With one exception (31m in 1983) the scallops from TNNP always differed from the Sunnyside and the Dildo samples. In the 31m comparisons only intercepts differed, whereas in the 10m and 20m samples either the slope or the intercept values were different. This was not unexpected in view of the large differences in the equations describing shell height, somatic weight and scallop age previously described. Thus not only did the TNNP scallops have less shell height and somatic weight per year of growth but also less body weight for individuals of given height. Differences were seen between Dildo and Sunnyside scallops at every depth on all occasions. The general trend, with two exceptions (10m in 1981 and 31m in 1983), was for these regressions to have similar slopes and different intercepts. These differences between Dildo and Sunnyside scallops were not surprising, in view of the similarities in the shell height versus age relationships and differences in the

somatic weight versus age relationships. Thus the scallops had the same shell height but a different somatic weight at any given age, so that the somatic weight versus shell height relationships were different, e.g. 10 year olds were the same height but a Dildo scallop had a greater somatic weight.

3.6.3. Annual Variation

Large sample sizes were not always obtained for some depths at the secondary sites. Only the primary sites, Sunnyside and Colinet, where reasonably large samples were collected for three consecutive years were compared in terms of annual variation in age-related rates of shell and somatic growth. Scallops less than five years old were occasionally scarce and therefore absent from some collections at the primary sites. This raised the possibility that any observed yearly differences between samples could be attributable to the underepresentation of young scallops in a particular year. The samples were first compared using all age classes (two to 19 years), and when any differences in parameters were observed the comparison was made again after omitting all the two to four year old scallops. The results of comparisons between shell growth rates calculated separately for each year are presented in Tables A-13 and A-14.

For each depth at least one of the parameters in the three comparisons between years was different, although no consistent trend, such as a particular year differing from the others, was seen. After the young scallops were omitted from the analysis, no differences were seen between any years for the two depths in Colinet or in the samples from 31m in Sunnyside. The 1983 scallop sample from 10m in Sunnyside was different from both the 1981 and the 1982 samples, which were similar to one another. Only one β_2 parameter remained significantly different between the annual samples collected from 20m in Sunnyside.

The results of comparisons between age specific somatic growth rates calculated separately for each year are presented in Table A-15. Significantly different parameters for different years were only seen for the Colinet 16m

samples (where 1981 was different from 1982 and 1983) and the Sunnyside 31m samples (where 1982 was different from 1981 and 1983). Even when scallops less than five years old were omitted (Table A-16), the same differences were evident between the Colinet 16m samples, whereas no significant annual variation was demonstrated in the Sunnyside 31m samples.

The strong influence of the younger year classes in this type of regression analysis was clearly demonstrated. Differences exhibited when all the age classes were combined could have been an artifact of unequal sample sizes. Alternatively, the small scallops may have growth rates which vary annually. If any part of the population were varying from year to year it would probably be the smaller and faster growing individuals, which may be more capable of taking advantage of favourable conditions. The differences observed were not consistent between depths or sites for any given year, so the former reason seems more likely than the latter, except for the three examples in which differences remained even after omission of the small scallops.

The simple linear relationships between somatic weight and shell height (both log transformed) were compared for all sites sampled for two or more years, and a summary of these comparisons is presented in Table A-17. The corresponding regression equations are given in Tables A-18 and A-19. Whereas very little annual variation was seen in age specific somatic growth rates, considerable year to year differences were recorded for some depths and sites. This type of analysis is particularly appropriate for determining whether there is annual variation in somatic weight, because it eliminates problems associated with accurately assessing age and reduces those caused by missing age classes or small sample sizes.

The only scallops displaying no annual variation in somatic weight versus shell height relationships were those samples from New Jersey and from 10m in Dildo. Regressions for Terra Nova scallops all possessed similar slopes but significantly different intercepts, and the Spencers Cove samples were also

different in every year studied. The general trend at Colliet was similarity of slopes (except for the 1981 and 1983 comparison in the 6m samples) and inequality of intercepts (with the exception of the 1982 and 1983 comparison between 16m samples). Samples from the year 1981 were different from those collected during 1982 and 1983 for 10m and 20m depths at Sunnyside and for 20m and 31m depths at Dildo. The samples collected from 31m in Sunnyside in the year 1982 were similar to those collected in 1981 and 1983, but there were differences in slope in the regressions describing Sunnyside data (31m) in 1981 and 1983.

3.7. Production Estimates

3.7.1. General

Since there was no annual variation in the somatic weight versus age relationships in scallops from identical depths at the same locations or in scallops from different depths at St. Andrews, an overall mean somatic weight for each age class was estimated from the polynomial equation fitted to the pooled yearly data (or depth data in the case of the St. Andrews samples). As a result of this the somatic production (Pg) values were identical for a particular depth at each location (or between depths in St. Andrews) and any annual variation in total production was due to variable Pr values.

Comparisons of somatic and prespawned gonad weight versus shell height regressions were made to determine if these relationships were different for each sex (Tables A-20,A-21). For the somatic weight data, only one of the 11 comparisons showed a significant difference between males and females. For the prespawned gonad weight data, males and females differed in nine of 30 comparisons made, but there were no trends of one sex consistently having heavier gonads per given shell length than the other. The data for males and females were therefore always combined for the estimation of both components of total production (Pg and Pr).

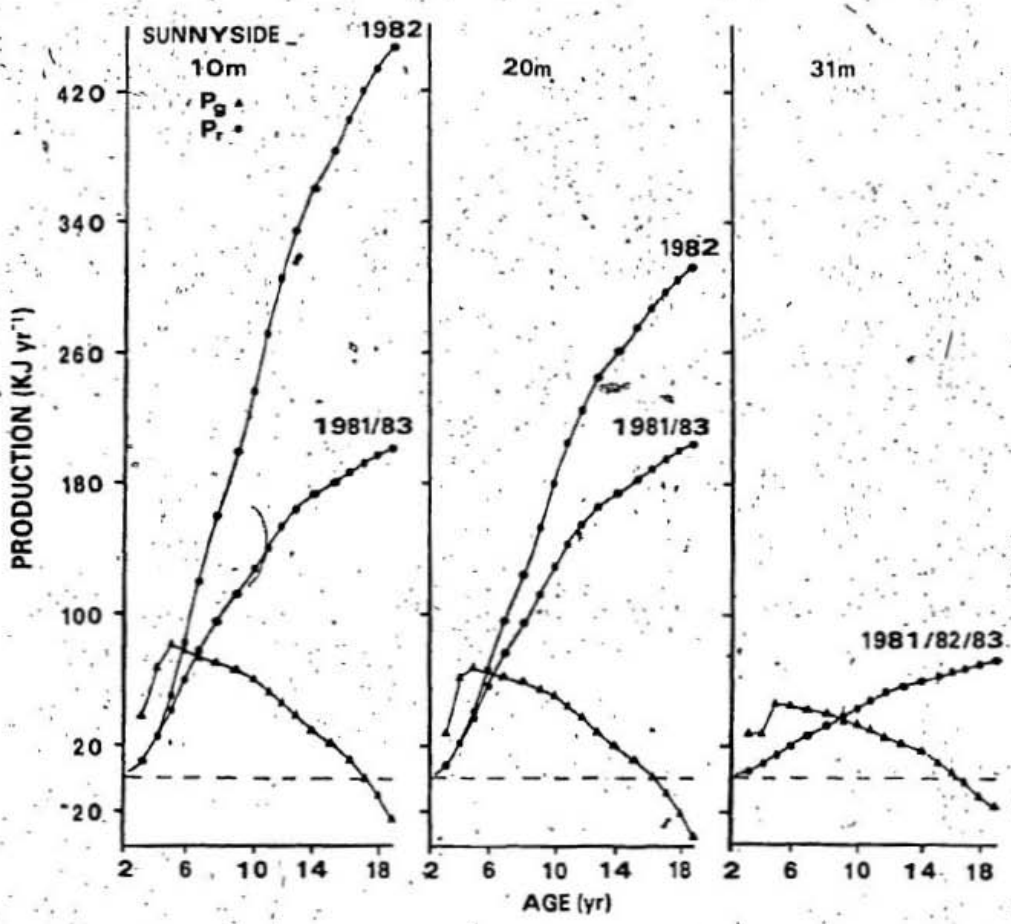


Figure 3-15: Age specific gamete and soma production in Sunnyside scallops.

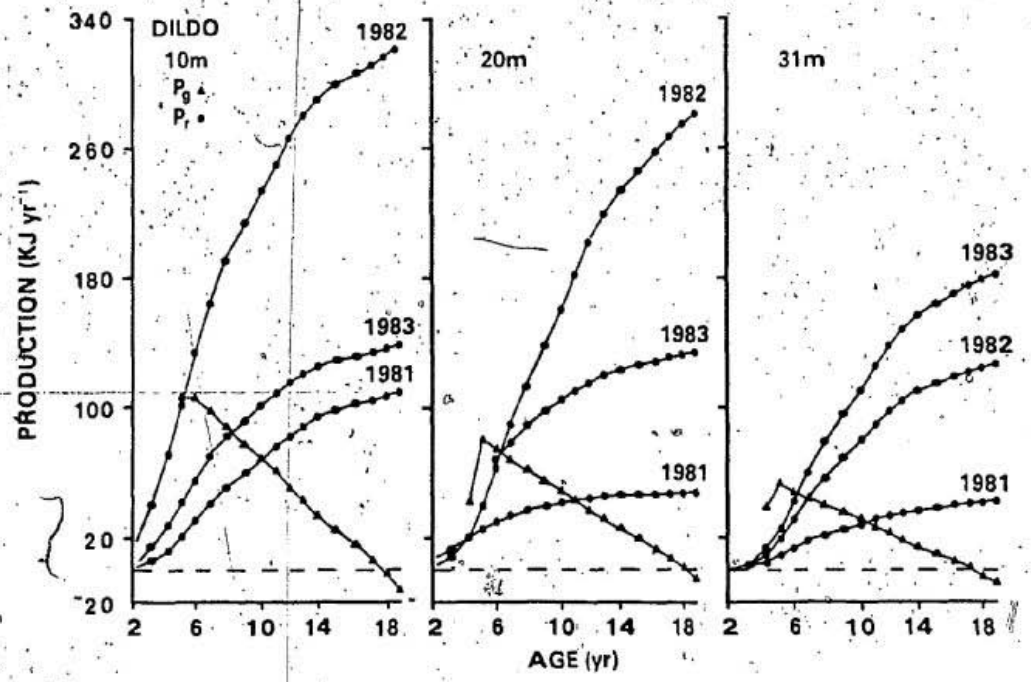


Figure 3-16: Age specific gamete and soma production in Dildo scallops.

The age specific values for Pr and Pg for Sunnyside, Dildo and TNNP are presented in Figures 3-15, 3-16 and 3-17 respectively. The corresponding values for samples collected in Colinet, New Jersey, St. Andrews and Spencers Cove are summarized in Figure 3-18. Estimates of total annual production for scallops collected in Sunnyside and TNNP are included in Table 3-4 whereas the corresponding values for Dildo are found in Table 3-5. Total production estimates for Colinet, Southern Harbour, St. Andrews, New Jersey and Spencers Cove are presented in Table 3-6.

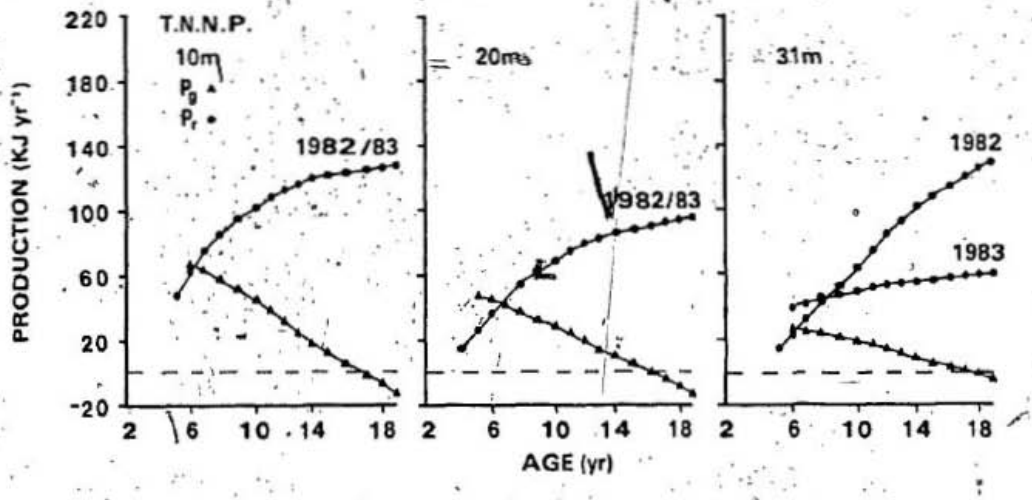


Figure 3-17: Age specific gamete and soma production in TNNP scallops.

The general trend for Pr was to increase steadily with age until an asymptote was reached (Figures 3-15, 3-16, 3-17, 3-18). Pg values increased rapidly during the first few years and, after reaching a peak at approximately four or five years of age, they steadily declined with age until the age of 17 or 18 when they became negative, owing to the decrease in body weight which occurs in older scallops, described in section 3.6.

Total production (Pg+Pr) increased with age during the earliest years, but after (Pg+Pr) reached a maximum a gradual decline in subsequent years was demonstrated in almost all the long-lived Newfoundland samples (Tables 3-4, 3-5,

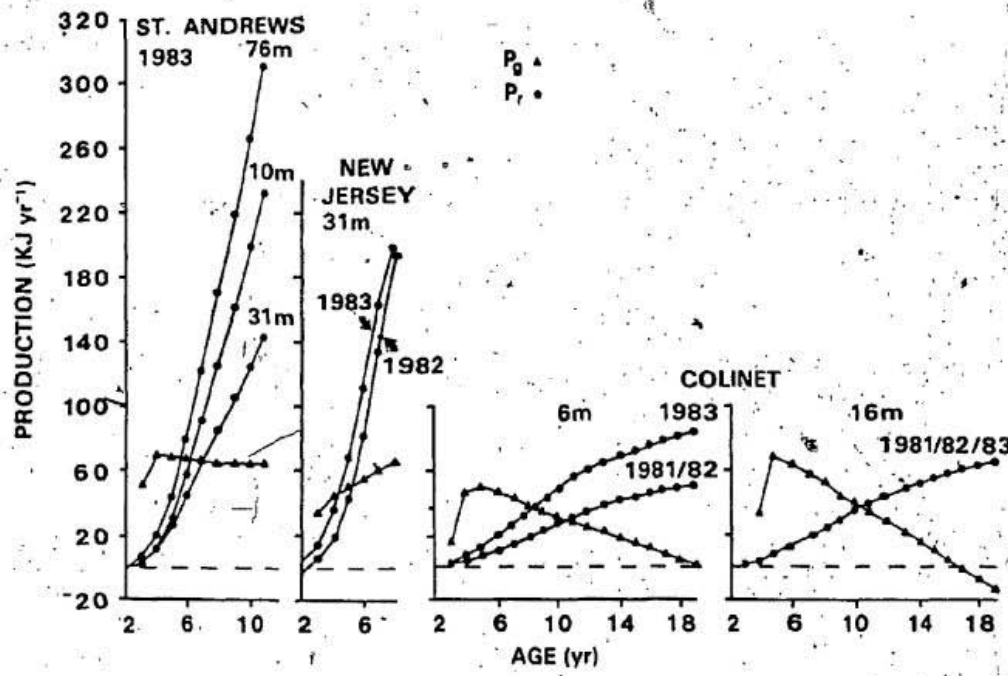


Figure 3-18: Age specific gamete and soma production in scallops from Colinet, New Jersey, St. Andrews and Spencers Cove.

3-6). Decreasing total production was a result of Pg declining faster than Pr was increasing. Exceptions included the Sunnyside 10m and 20m samples collected in 1982, in which Pr was increasing at a faster rate than Pg was declining, and the 1983 Southern Harbour sample, which did not display negative somatic growth.

Table 3-4: Summary of total production values ($Pg+Pr;kJ\ yr^{-1}$) for samples from all depths and years at Sunnyside and TNNP.

	SUNNYSIDE					TERRA NOVA			
Age	10m		20m		31m	10m	20m	31m	
	(81/83	82)	(81/83	82)	(81/82/83)	(82/83)	(82/83)	(82	83)
3	50	47	36	34	35				
4	93	92	83	82	38				
5	124	132	106	109	61		76		
6	139	161	123	133	66	130	82	50	66
7	153	194	140	159	70	140	87	59	70
8	166	229	155	186	74	144	92	68	70
9	178	265	168	209	76	147	95	76	69
10	187	298	180	231	78	147	97	84	69
11	194	327	188	249	80	147	98	92	69
12	198	353	193	263	80	145	98	99	68
13	201	375	196	275	78	143	97	105	67
14	202	392	197	282	77	139	96	110	65
15	200	406	195	287	74	135	94	115	64
16	197	416	191	288	71	131	92	119	62
17	192	423	185	287	65	125	89	122	61
18	184	425	178	283	61	121	86	125	59
19	176	426	168	277	55	115	83	127	57

Table 3-5: Summary of total annual production values ($Pg+Pr; kJ\ yr^{-1}$) for each depth sampled at Dildo during 1981, 1982 and 1983

DILDO

	10m			20m			31m		
Age	81	82	83	81	82	83	81	82	83
4				62	65		44	49	52
5	128	212	150	106	122		63	74	79
6	138	245	164	104	138		63	81	92
7	139	263	168	102	157	142	62	88	105
8	139	280	171	99	175	151	62	97	119
9	139	294	172	95	193	153	61	104	132
10	139	306	172	91	210	154	60	110	143
11	137	314	170	86	225	154	58	115	153
12	135	320	167	81	239	153	57	119	161
13	132	324	164	77	250	151	54	122	167
14	127	324	159	71	258	149	51	123	171
15	123	325	154	65	264	145	49	123	174
16	118	323	147	60	269	142	45	123	176
17	112	320	141	54	273	138	42	122	176
18	106	317	134	48	275	133	38	120	176
19	98	312	127	43	276	129	34	118	175

Table 3-6: Summary of total annual production values ($P\bar{g}$+Pr;kJ yr^{-1}) for Colinet, Southern Harbour, St. Andrews, New Jersey and Spencers Cove.

	SOUTHERN									SPENCERS	
	COLINET			HARBOUR	ST. ANDREWS			NEW JERSEY		COVE	
Age	(6m	6m	16m)	(10m)	(10m	31m	76m)	(31m	31m)	(10m	10m)
	81/82	83	81-83	83	83	83	83	82	83	81/83	82
3	16	18		44	55	57	57	39	48	103	112
4	37	52	37	80	82	82	89	62	80	109	124
5	67	62	76	94	98	95	112	92	118	120	140
6	56	65	75	107	124	112	147	136	167	128	152
7	57	69	75	123	155	130	188	193	223	134	160
8	57	72	75	141	190	151	235	260	263	137	165
9	58	77	74	159	226	170	283				
10	58	79	74	175	262	188	329				
11	58	82	73	192	296	205	374				
12	59	84	72	199							
13	58	85	70	228							
14	57	86	67	232							
15	56	87	65	243							
16	55	86	62	251							
17	53	86	57	258							
18	50	85	54	264							
19	49	84	50	269							

3.7.2. Annual Variation

The prespawn and postspawn gonad weight versus shell height regressions were compared for each depth and site in every year sampled to determine if these relationships varied annually. Where no annual variation was demonstrated for a particular depth and location, common regressions were then calculated to estimate gonad weight loss on spawning.

Variable prespawning gonad weights for scallops collected from Sunnyside (10m, 20m) and Spencers Cove (10m) resulted in higher values for Pr and total production in 1982 than in 1981 and 1983 (Table A-22). Annual variation was not observed in the Sunnyside (31m), Colinet (16m) or the TNNP (10m, 20m) samples, resulting in common values for Pr and total production. Year to year variation in Pr and (Pg+Pr) was observed at all sample depths in Dildo and in 31m from both Terra Nova and New Jersey. The samples obtained in 6m at Colinet were similar in 1981 and 1982 but significantly different in 1983.

The postspawn gonad weight versus shell height relationships were generally similar between years; e.g. in 18 of the 28 comparisons there were no differences at all (Table A-23). When samples from a single year were different from the other two years, no site, depth or yearly trends emerged, e.g. 1981 was a unique year for Colinet (6m) and Dildo (31m) whereas 1983 was the only different year for the Spencers Cove (10m) and Sunnyside (20m) samples. The regression parameters and statistics for prespawn and postspawn gonad weights versus shell height (both log transformed) are presented in Tables A-24 to A-27.

With the exception of New Jersey (31m), Dildo (31m) and Colinet (6m), where Pr was greater in 1983 than 1982, the Pr values for 1982 were at least as great as those from other years at all sites. A secondary trend seen in those sites sampled over a period of three years was for very high values of Pr in 1982 and lower but similar Pr values for 1981 and 1983, as in the Dildo (10m) example, or for no significant differences at all between 1981 and 1983, e.g. at Sunnyside (10m, 20m) and Spencer's Cove (10m).

Large annual fluctuations were characteristic of the shallowest depths from the more productive sites, such as Sunnyside, Dildo and Spencers Cove, in contrast to less productive sites such as TNNP and Colinet. More detailed comparisons of annual production between the various sites will be made in section 3.7.4.

3.7.3. Differences Related to Water Depth

Scallops collected from the shallowest depths in Sunnyside, Dildo and TNNP all had higher age-specific Pg values than those sampled from greater depths at the same sites. The one exception was the greater annual somatic growth exhibited by scallops collected from 16m in Colinet compared with those collected from 6m. Comparisons of somatic weight versus shell height relationships for different depths at a given site were included in section 3.6.1.

Greater age specific reproductive output (Pr) was demonstrated for the shallower samples (10m,20m) in Sunnyside. In each year the slopes for prespawned gonad weight versus shell height were similar for all three depths (Table A-28). The intercepts were always similar for the samples from 10m and 20m but the intercepts for the 31m samples were always different compared with the two shallower depths. Values for total production in Sunnyside were much greater at 10m than at 20m or 31m.

With the exception of 1983, when Pr was greater in scallops from 31m, a general trend of higher Pr values in the shallowest sample depths was also demonstrated for the Dildo data (Figure 3-16, Table 3-5). In 1981 only the data from 10m and 31m differed in intercept, whereas in 1982 all combinations were different. In 1983 the 10m and 20m samples were not significantly different from one another, but both had different slopes when compared with the 31m sample. With the exception of a very productive sample from 31m in 1983, total production declined with increasing water depth.

There was no clear trend in Pr at different depths in the TNNP samples, which were relatively similar (Figure 3-17, Table 3-4). In 1982 the scallops collected in 31m exhibited the highest Pr values, whereas they had the lowest in 1983. No differences in the gonad weight versus shell height relationships were observed in 1983, but they all differed in slope in 1982. With the exception of the 1982 sample from 31m, a general decrease in total production with depth was demonstrated in the TNNP data.

No clear depth related trends in Pr were displayed in the Colinet scallops (Figure 3-18, Table 3-6), although the gonad weight versus shell height regressions were identical only in 1982. Greater values of (Pg+Pr) were obtained in deep water scallops except in 1983, although these differences between depths in age specific total production at Colinet were very small.

Greater age specific values for Pr and total production were also observed in scallops from the greatest depth (76m) at St. Andrews (Figure 3-18, Table 3-6). Those from 10m at St. Andrews had a greater gonad output and total production than those from 31m. Only the 10m and 31m samples differed in their gonad weight versus shell height regressions.

3.7.4. Site Related Differences

The corresponding Pg values for each depth were slightly higher in Dildo than Sunnyside scallops, but values for the TNNP samples were lower than those for the aforementioned sites (Figures 3-15, 3-16, 3-17). Comparisons of somatic weight versus shell height relationships for corresponding depths at each of these sites have been presented in section 3.6.2, but the summary of the statistical comparisons of prespawned gonad weight for similar depths at each site are presented in Table A-29.

In 1981 greater Pr and total production values were observed for scallops from each depth at Sunnyside than for those from comparable depths at Dildo

(Figures 3-15, 3-16, Tables 3-4, 3-5). The prespawned gonad weight versus shell height relationships were different for both the 10m and 31m samples, but despite the much higher Pr values observed for the Sunnyside 20m sample there was no difference from the 20m Dildo sample, which may be related to the poor regression (see Table A-24) obtained for the Dildo sample.

In 1982 greater values for Pr and total production were observed in the Sunnyside 10m and 20m samples than in Dildo or TNNP. Similar Pr values were seen in the 31m samples from all three sites but there was greater total production in scallops from Dildo and TNNP compared to Sunnyside. The gonad weight versus shell height relationships for the 10m samples were different for each site, whereas the 20m samples from Sunnyside and Dildo were identical, and both had intercepts that differed from the TNNP sample. There were no differences in gonad weight versus shell height between Dildo and Sunnyside or TNNP scallops, but Sunnyside and TNNP samples were different.

In 1983 greater values for Pr and total production were found in the Sunnyside 10m and 20m samples than Dildo or TNNP collections made in similar depths. Whereas greater Pr and total production estimates in the 31m samples were observed at Dildo, the Sunnyside and TNNP samples were similar. The gonad weight versus shell height relationships between 10m samples were similar for Dildo and Sunnyside or Terra Nova, but Sunnyside and TNNP were different from one another. Comparisons of 20m samples revealed similarities between Sunnyside and Dildo, but both of these differed from TNNP, whereas the 31m sample from Dildo was different from both the Sunnyside and the TNNP samples, which were identical.

If comparisons were made with the Colinet data, for which 6m was considered equivalent to 10m, then Pr values and total production estimates for any given year were less than those obtained at other sites, especially Sunnyside and Dildo. If 16m were considered to be approximately equivalent to 20m, then Colinet scallops always produced fewer gametes and had lower total production

than any other sites in any given year, with the exception of 1981, when they were similar to Dildo scallops.

3.8. Reproductive Effort, Value and Cost

3.8.1. Reproductive Effort

Values for age specific reproductive effort (RE) and size specific RE for the primary sites (Sunnyside and Colinet) are presented in Figure 3-19. Data were pooled where appropriate e.g. when there was no annual variation in Pr.

Greater RE values were observed in 1982 than in 1981/83 at Sunnyside (10m and 20m data combined), but in 6m at Colinet RE was greatest in 1983. Maximum RE values were observed at approximately 16 years of age before the values calculated by $RE=[Pr/(Pr+Pg)]\cdot 100$ exceeded 100% due to negative Pg values, also observed in sea urchins by Thompson (1983). The Colinet 6m samples were an exception because they did not display declining somatic weight during the final years.

At Sunnyside in every year age specific RE was greater at 10m and 20m than at 31m. A similar depth trend was not observed in the Colinet data, where RE at 6m in 1983 was greater for scallops below approximately age 15 than RE at 16m, but was similar or lower in 1981/82. With the exception of the eight to 14 year old scallops collected from 6m in Colinet during 1983, RE values for all the Sunnyside samples were higher than those from Colinet, especially at comparable depths.

The scallops from shallower water in Sunnyside (10m, 20m) have been previously shown to be larger and heavier than those of comparable age from deeper depths (31m) and those from Colinet. It is therefore also desirable to compare the partitioning of energy between growth and reproduction in scallops of similar weight as well as in those of similar age. The same trends between depths and sites observed for age specific RE were also seen when weight specific RE was considered (Figure 3-19).

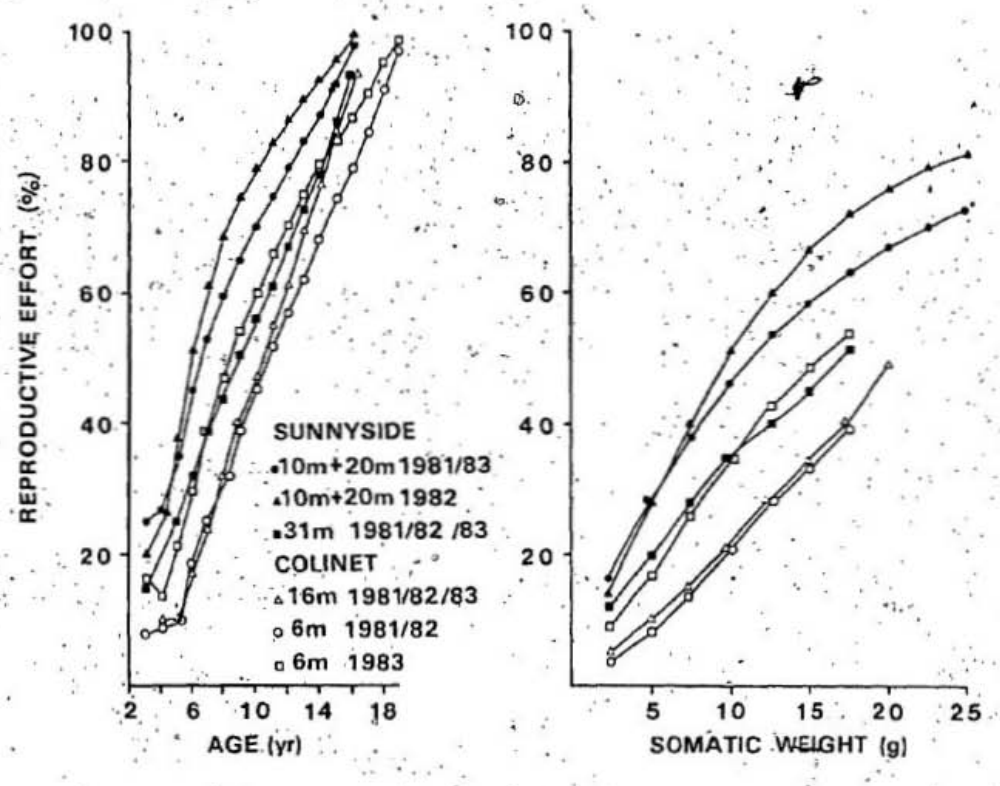


Figure 3-19: Age specific reproductive effort and size specific relative effort in Sunnyside and Colinet populations.

The scallops from shallow water at Sunnyside not only had higher age specific and weight specific reproductive output but also had greater proportions of their total production invested in gamete production, i.e. a higher RE.

The amount of energy invested in gamete production expressed as a proportion of ingested or absorbed ration, or as a proportion of the total energy budget, has also been proposed as an alternative index of reproductive effort (Hirshfield and Tinkle,1975; Calow,1979). The first step in this procedure was to calculate monthly clearance and metabolic rates for Sunnyside scallops from 10m and 31m, using the slopes obtained for the clearance rate versus total dry weight regression (0.69) and metabolic rate versus total dry weight regression (0.89; Section 3.3). This was done for scallops of standard dry weights which lay within the range found in each population (5-40 g at 10m, 5-20 g at 31m). Monthly rates of ingestion were then calculated by multiplying the appropriate clearance rate (l hr^{-1}, by the corresponding ambient food availability that month (J l^{-1}) for each depth and the number of hours per month. The sum of the monthly values gave the total energy ingested per year. Annual metabolism was the sum of monthly oxygen consumption rates calculated by multiplying the appropriate values (ml O_2 hr^{-1}) by a conversion factor (19.9 J ml^{-1} O_2 and by the number of hours per month. Pr and Pg for each size and depth were obtained by estimating the age of each scallop of given standard total weight and interpolating the corresponding Pr and Pg values from the curves in Figure 3-15.

Whereas the physiological measurements were only made in 1983, an additional comparison was made by applying the same seasonal metabolic and clearance rates to the 1982 data. The annual totals for ingestion and expenditure of energy expressed in kJ yr^{-1} for 1982 and 1983 are summarized in Table 3-7.

Different levels of food availability resulted in greater annual ingestion rates for the scallops collected from 10m in 1982 than comparably sized scallops from 31m, but ingestion rates for scallops from both depths were similar in 1983. Both the Pr and Pg values were lower at 31m than at 10m but the values for the 31m

Table 3-7: Cumulative totals for ingested ration I, somatic production Pg, gamete production Pr and O_2 consumption for a series of standard-sized scallops from 10m and 31m at Sunnyside. All values are expressed in kJ yr^{-1}.

10m

Total Weight	1982 I	1982 Pr	1982 Pg	1982 O_2	1983 I	1983 Pr	1983 Pg	1983 O_2
5 g	509.8	18.5	50.8	111.8	388.1	21.5	57.0	111.8
10 g	852.7	49.7	81.8	207.8	620.2	42.0	81.8	207.7
15 g	1096.9	82.2	78.7	297.9	834.9	70.2	86.5	297.9
20 g	1354.8	120.2	74.7	385.0	1030.5	112.3	68.0	385.0
30 g	1786.6	219.2	62.5	551.9	1365.6	140.9	53.2	551.9
40 g	2072.5	307.5	45.8	663.2	1584.1	186.7	10.04	663.2

31m

5 g	335.1	15.2	46.3	85.5	396.7	15.2	46.3	85.5
10 g	526.5	27.1	42.9	158.7	631.4	27.1	42.9	158.7
15 g	721.8	43.9	34.6	227.5	854.1	43.9	34.6	227.5
20 g	884.4	66.1	4.9	291.4	1046.2	66.1	4.9	291.4

Table 3-8: Corresponding values for gamete and somatic production at Sunnyside, plus O_2 consumption, expressed as a percentage of ingestion (·100).

Total Weight	1982 Pr/I	1982 Pg/I	1982 O_2/I	1983 Pr/I	1983 Pg/I	1983 O_2/I
			10m			
5 g	3.62	9.97	21.92	5.54	14.69	28.80
10 g	5.83	9.60	24.37	6.78	13.19	33.50
15 g	7.49	7.17	27.15	8.40	10.36	35.68
20 g	8.87	5.52	28.42	10.90	6.60	37.36
30 g	12.27	3.50	30.90	10.32	3.89	40.41
40 g	14.84	2.21	32.00	11.78	0.63	41.81
			31m			
5 g	4.52	13.82	25.52	3.82	11.67	21.56
10 g	5.15	8.14	30.15	4.30	6.79	25.15
15 g	6.08	4.79	31.52	5.14	4.05	26.64
20 g	7.47	0.55	32.95	6.32	0.47	27.86

scallops were the same for 1982 and 1983 owing to a lack of annual variation in total production for this site and depth (Section 3.7.2). Lower Pg values were observed for the 31m scallops because they were much older than those of equivalent weight collected from 10m. Thus a 20 g scallop from 31m was approximately 17-19 years of age whereas one from 10m was only seven or eight years old and still growing relatively quickly. Higher Pg values were also observed in 1982 than in 1983 for the heavier (>30 g) scallops from 10m for the same reason ,i.e. a 20 g animal was approximately eight and a half years old in 1983 but only seven years old in 1982. Much higher gonad weights resulted in younger scallops achieving a given equivalent weight in 1982. Higher rates of oxygen consumption were observed for the faster growing scallops from 10m.

The annual cumulative Pr, Pg and O_2 consumption for 1982 and 1983, expressed as percentages of total ingestion, are presented in Table 3-8. In each year scallops from 10m invested a greater proportion of their ingested ration in the production of gametes and somatic tissue than scallops of similar weight collected from 31m (with the exception of 5 g scallops from 31m in 1982). Although the ingested ration for the 10m scallops was higher in 1982, they invested a greater proportion in gamete production than they did in 1983, but the proportion spent on somatic tissue growth was lower in 1982. The similar rates for gamete, soma production and oxygen consumption for the 31m collections in 1982 and 1983 resulted in a simple inverse relationship between these three quantities and total ingestion. For example, in 1983 when the ingested rations of 31m scallops were higher than in 1982, the equivalent production and metabolic loss estimates represented a smaller proportion of the total than they did in 1982. Metabolic expenditure as a proportion of ingested energy in the 10m samples was lower in 1982 due to higher ingested ration in that year, which may have also contributed to lower Pg values in 1982.

The percentages of ingested ration invested in gamete production, somatic production and oxygen consumption (Table 3-8) were also expressed as functions

of age (Figure 3-20). The proportion invested in growth ranged between 10% and 14% for four year olds, and declined rapidly with age to zero around 14 or 15 years of age in the 31m scallop collections. In the 10m scallops during 1983, somatic production was still positive (1%) at age 16 because the scallops were still growing, albeit slowly. Somatic production could not be calculated for the 10m samples beyond 12 years because the range of standard size animals only included those up to 40 g total weight.

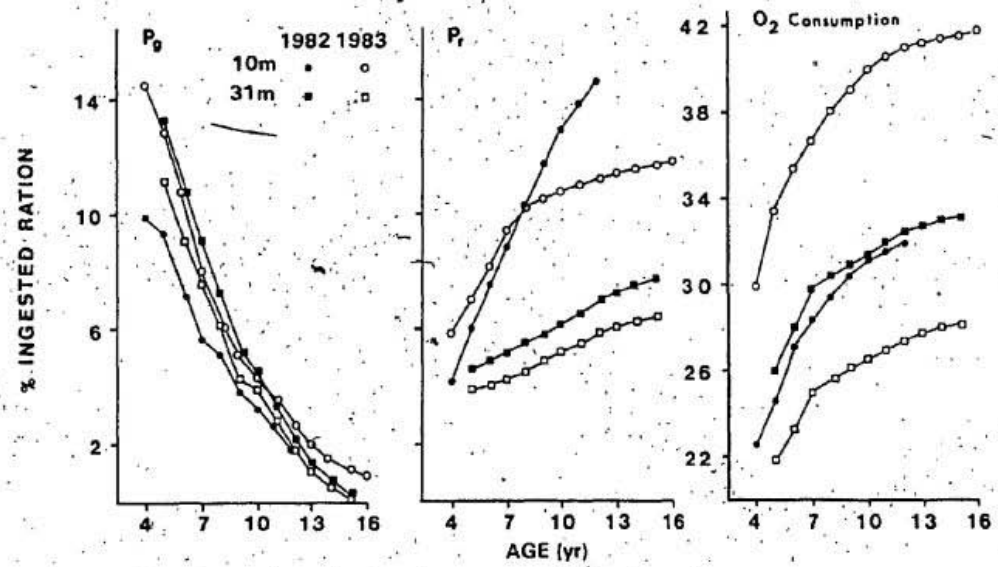


Figure 3-20: Age specific gamete and somatic production, plus oxygen consumption expressed, as a percentage of ingested ration (·100).

The proportion of ingested energy invested in gametes steadily increased with age for both populations with generally higher 1982 values from corresponding depths. In each year, consistently higher values were observed in the 10m collections.

Oxygen consumption as a percentage of ingested ration increased from approximately 22-30% to 28-42%, depending on depth and year, with values for the 10m samples at least similar to (1982) or much greater than (1983) those for the 31m samples. Annual differences at each depth are attributable to variations in ingested ration, because the same oxygen uptake data were used in each year.

3.8.2. Reproductive Value

Reproductive value, expressed in terms of fecundity, was calculated from the mean weight per million scallop eggs and the age specific weight loss on spawning. The mean weight (g) per million scallop eggs for both depths combined was 0.115± 0.023 in 1982 and 0.091± 0.016 in 1983. Reproductive value was also expressed as the energy invested in gamete production (Pr) (Figure 3-21).

Since fewer scallops were used for the mortality study in Sunnyside than in Colinet, and the number of scallops that died at the former site was insufficient to calculate a separate mortality curve, the mortality curve for the Colinet population (Figure 3-11) was used to calculate age specific survivorship for scallops from Sunnyside. Identical age specific mortality rates, rather than size specific rates, were used for the 10m and 31m scallops, on the assumption that scallops of equal age from the two depths at the same location were more likely to have similar mortalities than similar-sized animals, because the scallops from 10m were much younger at any given size.

Common survivorship probabilities for the 10m and 31m samples, and the products of these values and age specific reproductive output for 10m (1981/83 and 1982) and 31m (1981-1983) respectively, are presented in Tables A-30 to

A-33. These products represent the future potential for producing offspring in terms of energy or residual reproductive value for each age class (Figure 3-21). The calculations take into consideration the probability of death from one year to the next and the increased reproductive output when each additional age is attained.

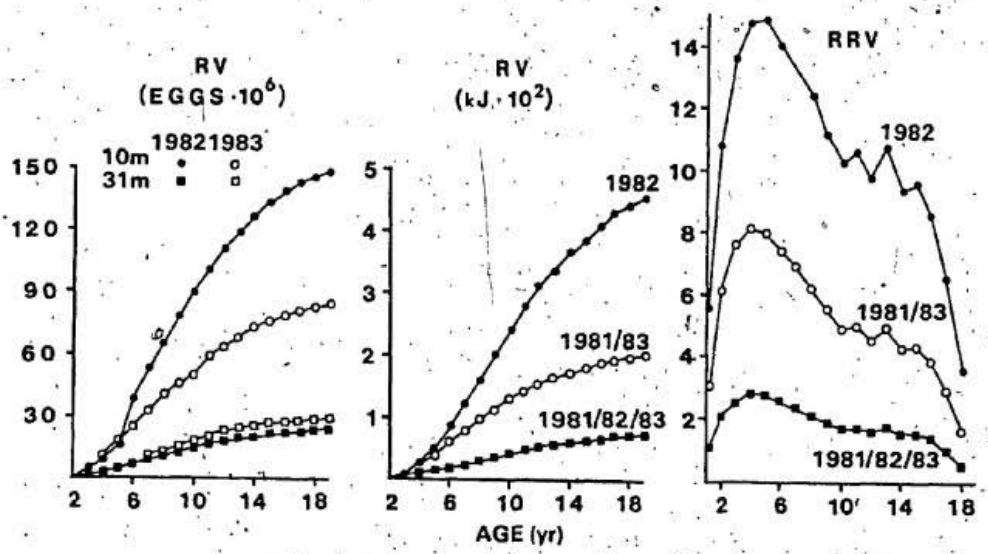


Figure 3-21: Reproductive value (RV) and residual reproductive value (RRV) for scallops from 10m and 31m at Sunnyside.

Reproductive value increased with age and was much greater for scallops from 10m than for those from 31m (Figure 3-21). Although individual eggs produced in 1982 were larger and heavier than those spawned in 1983, fecundity (egg numbers) was greater in the latter year, and reproductive output (Pr) was the same in both years. For the same reason the differences in fecundity between the 10m samples were not as great as the differences in reproductive output. RRV values for all three conditions increased to a maximum at approximately four or five years of age, then declined rapidly until about age 10. The slow declines between the years 10 and 16 were probably due to the low probabilities of death almost being offset by the increasing reproductive output. The further rapid decline was a result of very high mortalities in the later years. RRV did not reach zero for these populations because there were some old individuals to which ages could not be confidently assigned. Regardless of age, RRV was much higher at 10m than at 31m owing to the compounding effect of higher age specific reproductive outputs over the entire lifespan.

3.8.3. Reproductive Cost

In order to estimate reproductive cost it was necessary to divide the annual reproductive cycle into non-gametogenic and gametogenic phases. To determine the separate phases, the weight of gametes in the gonads of standard 140mm scallops from 10m and 31m in Sunnyside were calculated for each month by multiplying mean gonad dry weights by the appropriate GVF (Figure 3-22). The gametogenic phase was from April to September inclusive at both depths. Similar increases in gonad weight and DNA content of the testis have previously been demonstrated in *Placopecten magellanicus* from Newfoundland for the same time of the year (Thompson,1977).

The values of oxygen consumption for the remaining six months (October to May; considered to be the non-gametogenic phase) were combined to calculate means for a series of standard sized scallops. An estimate of the metabolic cost of maintaining somatic tissue (R^*) was obtained by multiplying this monthly average

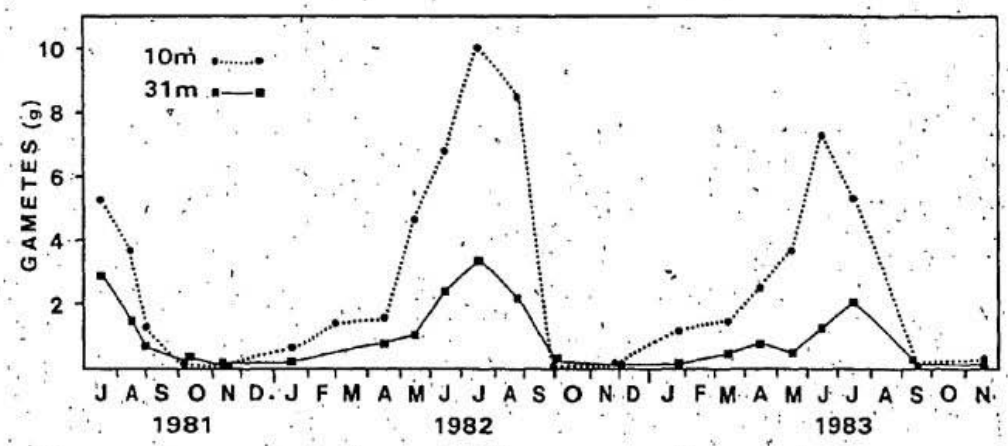


Figure 3-22: Seasonal cycles in the total weight of gametes in the gonad of a standard 140 mm scallop from 10m and 31m at Sunnyside.

by 12. Values for Pr and total metabolism (R) were obtained from Table 3-7. Values for C (consumption) were obtained by multiplying the annual ingestion rates (Table 3-7) by a mean annual absorption efficiency (e) of 0.47 (Thompson, pers. comm.). Reproductive cost was then calculated as described in Section 2.9.2, and results presented in Tables 3-9 and 3-10 and Figure 3-23.

Only in large (>20 g) scallops from 10m in 1983 did the production of gametes and the associated metabolic expense divert energy away from the maintenance of somatic tissue, i.e. there was a positive value for reproductive cost. In this circumstance the larger scallops may be considered *reckless* (Calow,1979). Reproductive output was much greater at 10m during 1982 than in 1983 samples but there was no reproductive cost, since ingested ration increased. Reproductive cost for the 31m scallops was lower in 1983, owing to higher ingestion rates, and did not attain positive values. Relatively greater costs (less

Table 3-9: Values for gamete production, absorbed ration and total metabolism partitioned into reproductive and nonreproductive components in 1982 for scallops from 10m and 31m at Sunnyside (1ml O_2=19.9 J).

1982

Total Weight	C*e	Pr	R	R*	R-R*	R*/R	Co*
10m							
5 g	239.6	18.5	111.8	80.4	31.3	0.72	-1.36
10 g	400.7	49.7	207.8	149.4	58.4	0.72	-0.96
15 g	515.6	82.2	297.9	213.4	84.5	0.72	-0.64
20 g	636.7	120.2	385.0	275.8	109.2	0.72	-0.48
30 g	839.7	219.2	551.9	400.6	151.3	0.73	-0.17
40 g	974.0	307.5	663.2	477.5	185.7	0.72	-0.01
31m							
5 g	157.5	15.2	85.5	62.4	23.2	0.73	-0.91
10 g	247.5	27.1	158.8	118.2	40.6	0.74	-0.52
15 g	339.3	43.9	227.5	167.4	60.7	0.74	-0.41
20 g	415.7	66.1	291.4	215.1	76.4	0.74	-0.27

negative) were observed in all the scallops as they grew (aged). In general, scallops from Sunnyside displayed *restraint* (Calow,1979) in their reproductive strategies.

Table 3-10: Values for gamete production, absorbed ration and total metabolism partitioned into reproductive and nonreproductive components for 1983 in scallops from10m and 31m at Sunnyside (1ml O_2=19.9 J).

1983

Total Weight	C*e	Pr	R	R*	R-R*	R*/R	Cost
10m							
5 g	182.3	21.5	111.8	80.4	31.31	0.72	-0.61
10 g	291.5	42.0	207.8	149.4	58.4	0.72	-0.28
15 g	392.4	70.2	297.9	213.4	84.5	0.72	-0.11
20 g	484.3	112.3	385.0	275.8	109.2	0.72	+0.05
30 g	641.8	141.0	551.9	400.6	151.3	0.73	+0.13
40 g	744.5	186.7	663.2	477.5	185.7	0.72	+0.22
31m							
5 g	186.5	15.2	85.5	62.4	23.2	0.73	-1.38
10 g	296.7	27.1	158.8	118.2	40.6	0.74	-0.94
15 g	401.4	43.9	227.5	167.4	60.1	0.74	-0.78
20 g	491.7	66.1	291.4	215.1	76.4	0.74	-0.62

3.9. Comparisons of Cultured and Natural Populations

The cultured scallops from Spencers Cove had greater shell heights and somatic weights at a given age when compared with naturally grown or wild scallops from nearby Southern Harbour (Figure 3-14). Von Bertalanffy equations indicated that the cultured scallops reached their smaller $H\infty$ of 127.6 mm at a much faster rate (k=0.38) than the naturally grown scallops, for which the Brody growth coefficient (k) was 0.16 and the asymptotic height $H\infty$ 173.8 mm.

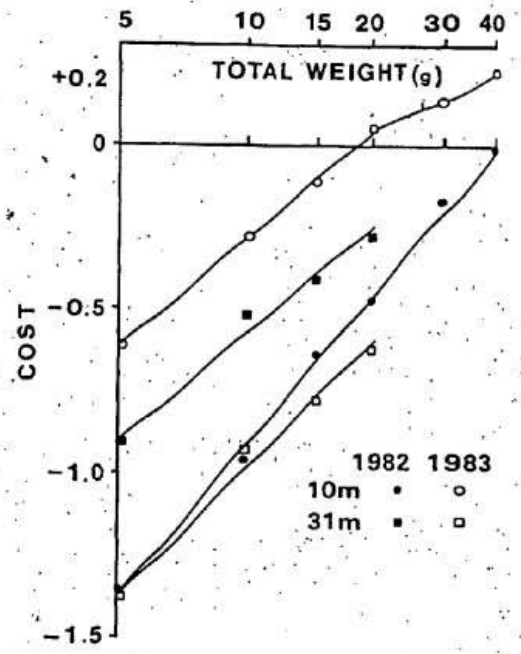


Figure 3-23: Reproductive cost in scallops from 10m and 31m at Sunnyside.

Cultured scallops greater than eight years of age were not available, so statistical comparisons between cultured and wild scallops were made on the age classes between two and eight years, which were common to both groups. All the parameters for the age specific shell height and somatic weight comparisons fitted to polynomials were significantly different (Table 3-11). Slopes for the shell weight and somatic weight versus shell height regressions were significantly different, with lower shell weights and higher somatic weights in a given height

class observed for the cultured scallops. There were no differences observed in the prespawned gonad weight versus shell height relationships for the two scallop samples collected in 1983.

Table 3-11: Summary of t values for comparisons of growth rates in cultured and naturally grown scallops. Cubic polynomials fitted to shell height versus age data; quadratic polynomials for somatic weight vs. age relationships; and somatic, prespawned gonad and shell weights all related to shell height.

	Shell Weight (age)	Somatic Weight (age)		Somatic Weight (height)	Gonad Weight (height)	Shell Weight (height)
β_0	9.41***	8.30***	a	–	0.32	–
β_1	3.57***	3.20***	b	5.60***	0.19	2.14*
β_2	4.33***	3.01**				
β_3	2.94**					

Age-specific comparisons of reproductive effort, gamete production and somatic production in addition to estimates of reproductive effort calculated on a weight basis which attempted to reduce the influence of the faster growth rate for cultured scallops are presented in Figure 3-24. The low H_∞ value and rapidly declining Pg values for the cultured scallops suggest they may not live as long as the wild scallops. In an attempt to reduce the influence of the age factor each age class expressed as a proportion of the total lifespan and its corresponding reproductive effort for the cultured and wild scallops was included in Figure 3-24. Longevity for the cultured scallops was estimated to be 12 years based on the length of time to reach the asymptotic length and by extrapolating the declining Pg values to zero. The lifespan of the wild scallops was estimated to be 20 years.

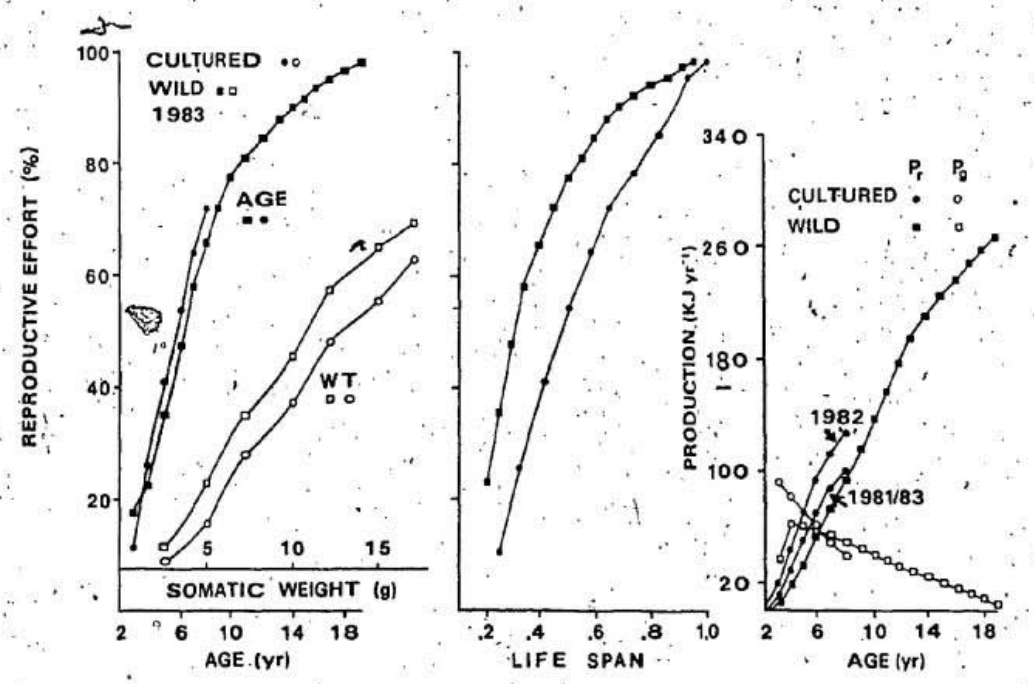


Figure 3-24: Age specific reproductive effort and production, relative size specific RE, and RE for each age class, expressed as a proportion of life span for cultured and natural populations.

Reproductive effort per given age class was higher in the cultured scallops, however after correcting for the effect of a more rapid growth rate effort was then greater for the naturally grown scallops. Greater values for reproductive effort

were also observed for the wild scallops when expressed as a proportion of the lifespan, for example, when the cultured scallops had achieved half of their expected lifespan they only had an effort of 54% whereas the naturally grown scallops had an effort of 77%. The values for gamete production per given age class were higher for the cultured scallops. The Pg values for the cultured scallops ranging in age up to six years were greater but lower than the wild scallops for age seven and eight indicating that the wild scallops were growing faster than cultured ones in the later years.

3.10. Comparison of Latitudinally Separated Populations

Scallops from approximately the northern and southern limits of distribution for *Placopecten magellanicus* were collected from Sunnyside and off the coast of New Jersey, respectively. Samples of scallops from an intermediate latitude were collected from St. Andrews, New Brunswick. The shallowest water from which scallops were routinely collected in the southerly New Jersey location was 31m. Since scallops were collected from more than one depth in Sunnyside and St. Andrews, a problem arose in selecting populations for meaningful comparisons between the three areas. The obvious choice would have been to compare samples collected in 31m, but the approach adopted here was to compare scallops from the shallowest depths at which they were found, because the annual cumulative day degrees were more similar to the warmer New Jersey environment in the northern shallow zones (10m) than in deeper water (31m). Statistical comparisons between the three locations were only made on those scallops collected in 1983, ranging in age from two to eight years.

3.10.1. Seawater Temperature

Water temperatures recorded at the New Jersey site were higher than at the two more northerly sites except during April to September (Figure 3-25). Temperatures in New Jersey averaged 17 °C in November but never dropped below 5 °C during the winter before gradually increasing between April and

September. Temperatures in St. Andrews dropped to zero in February and rapidly increased between April and June before leveling off to a maximum of 12 ° C in September. Temperatures in Sunnyside were lower than those observed in St. Andrews, especially during March and April, when they dropped below zero, but the general shape of the seasonal cycles were similar for these two sites. Annual day degrees were estimated as 3180 for New Jersey, 2536 for St. Andrews and 1451 for Sunnyside.

3.10.2. Gametogenic Cycles

Histological sections of gonad tissue were not obtained from scallops collected in St. Andrews but were available from scallops collected in New Jersey and Sunnyside on a monthly basis in 1982 and 1983. Scallops from Sunnyside spawned during late August, whereas the New Jersey population released their gametes in early or mid-October (Figure 3-26). Scallops from the Bay of Fundy area spawned during late August or early September (Dickie,1953). The proportion of mature gametes displayed the same trend as total gametes from July to November, but mature sperm rapidly increased in the gonads of New Jersey scallops from January through April while no mature sperm were observed during these months in Sunnyside samples. Mature and developing gametes declined and subsequently increased in proportion in the New Jersey samples during the summer months. This apparent release of mature gametes and the increase in developing gametes may be indicative of partial or dribble-spawning (Newell et al., 1982), so that my values for Pr and RE for the New Jersey scallops may be underestimates. Except during November to January, mature sperm were present in New Jersey scallops from February to October, even though the major spawning did not take place until October. In contrast, mature sperm were only present in Sunnyside scallops from April to September, corresponding to the gametogenic phase of the reproductive cycle described in section 3.8.3.

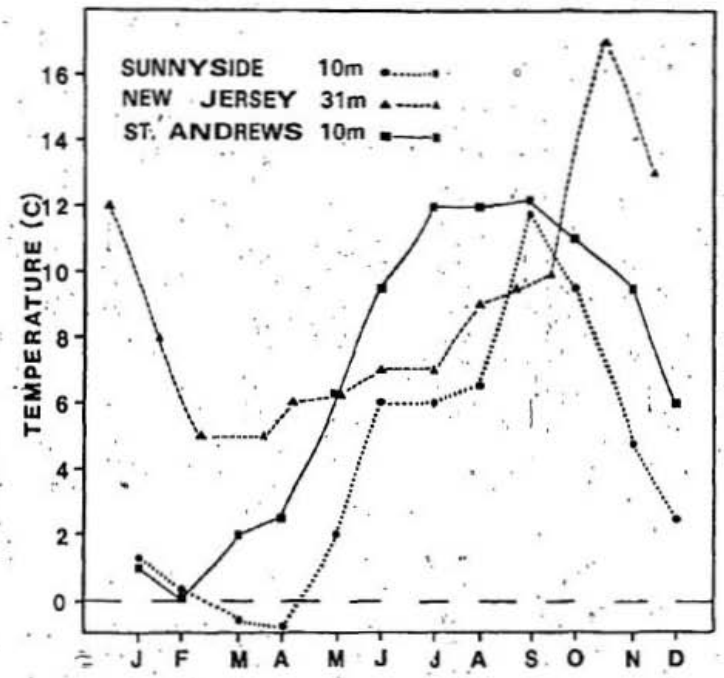


Figure 3-25: Seasonal cycles of mean monthly water temperatures for New Jersey, St. Andrews and Sunnyside.

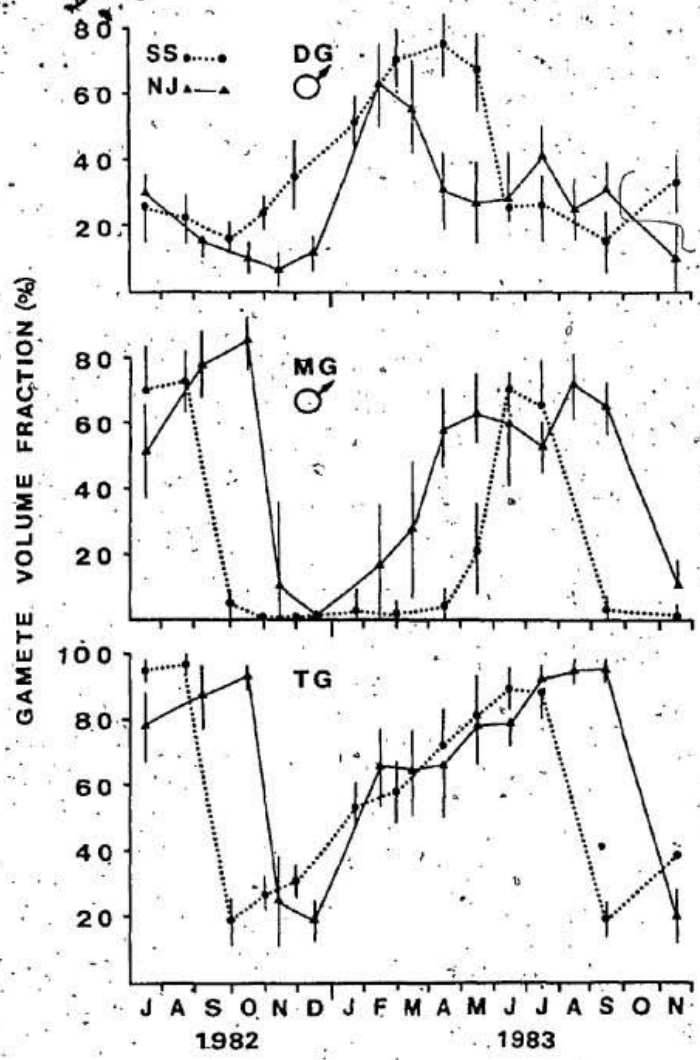


Figure 3-26: Gamete volume fractions for total gametes (TG) in males and females combined, and in mature (MG) and developing gametes (DG) calculated for male scallops from Sunnyside and New Jersey.

3.10.3. Growth Rates and Production

The Von Bertalanffy equations for all the age classes found in New Jersey, St. Andrews and Sunnyside were included in Figures 3-13 and 3-14. Despite high r^2 values for all three populations, the 95% confidence intervals for $H\infty$ were much greater for the New Jersey population (±20.8 mm) than either the St. Andrews (±12.5 mm) or the Sunnyside (±3.0 mm) populations. The lack of older scallops approaching asymptotic height in the New Jersey collections may have been responsible for a poor fit obtained by the Von Bertalanffy equation, resulting in a possible overestimate of $H\infty$ and underestimate of k. Scallops from Sunnyside are known to live at least 20 years (this study), whereas the longevity for scallops from the St. Andrews area or the Bay of Fundy generally does not exceed 12 years (Chandler, pers. comm.; Stevenson and Dickie, 1954). Only one ten year old scallop was found in the New Jersey collections. A general trend of lower k values but greater longevity and $H\infty$ values for the more northerly populations was obscured by the relatively small sample sizes from New Jersey and the resulting poor fit by the Von Bertalanffy equation. For example, a k value of 0.34 and $H\infty$ of 141.4 mm were reported for scallops up to age nine from the Georges Bank (cited in Naidu, 1969).

There were no significant differences between the shell height, somatic weight and age relationships (polynomials) in the three scallop populations, despite apparently lower age specific somatic weights observed in the New Jersey sample (Figure 3-27 and Table 3-12). The slopes for shell weight versus shell height equations were different for all three populations (Table 3-12). Similar slopes for the somatic weight versus shell height regressions were observed for all examples, but the New Jersey samples had a lower intercept than samples from both St. Andrews and Sunnyside, which were the same. Pg values were highest in Sunnyside scallops and lowest in those from New Jersey but the differences are not likely to be significant because of similarity in the somatic weights in each age class. The gonad weight versus shell height relationships were not significantly different between Sunnyside and New Jersey scallops but both of these

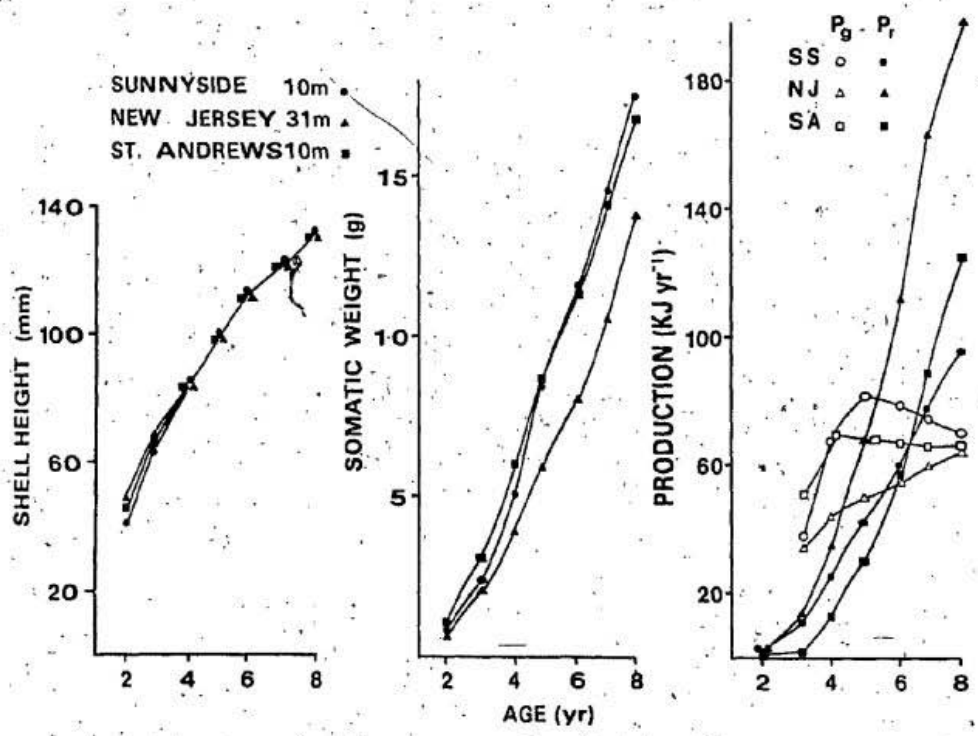


Figure 3-27: Age specific estimates of mean shell height, mean somatic weight, gamete production and somatic production for scallops collected from Sunnyide, St. Andrews and New Jersey.

populations differed from St. Andrews scallops. Scallops from New Jersey produced more gametes than scallops of similar age collected at Sunnyside or New Jersey.

Table 3-12: Summary of t values for comparisons of cubic polynomials fitted to shell height versus age; quadratic polynomials fitted to somatic weight versus age; and somatic, gonad and shell weight versus shell height, for scallops collected from Sunnyside, New Jersey and St. Andrews in 1983.

		Sunnyside+N.J.	N.J.+St.Andrews	Sunnyside+St.Andrews
Shell Height (age)	β_0	1.43	1.82	0.33
	β_1	1.30	1.47	0.03
	β_2	1.00	1.36	0.29
	β_3	0.87	1.31	0.39
Somatic Weight (age)	β_0	0.12	0.19	0.05
	β_1	0.15	0.00	0.20
	β_2	0.57	0.62	0.02
Shell Weight	a	-	-	-
	b	3.58***	3.10**	6.30***
Somatic Weight	a	8.96***	10.12***	0.67
	b	1.15	0.12	1.53
Gonad Weight	a	2.32	-	6.52***
	b	0.35	2.54*	2.22

3.10.4. Reproductive Effort

Reproductive effort in any given age class and the relative effort for a scallop with a standardized somatic weight (Figure 3-28) were both greater in the New Jersey population due to greater Pr and lower Pg values than in St. Andrews and Sunnyside scallops. Reproductive effort was greater in young scallops from Sunnyside compared with those from St. Andrews, but lower in older ones (>6 years). Relative effort values for scallops with similar somatic weights were consistently higher for Sunnyside scallops than for those from St. Andrews. Thus the relative effort of a 15 g scallop from New Jersey was >80%, whereas a Sunnyside scallop of the same weight only had an effort of 55%. This may be related to the fact that at 15 g the Sunnyside scallops had only attained half their maximum weight and were still growing rapidly, whereas the New Jersey scallops had almost achieved their maximum weight and were growing at a relatively slow pace. Due to different longevities in the three scallop populations, i.e. 20 years at Sunnyside, 12 years at St. Andrews and approximately 10 years at New Jersey, a correction previously described (Section 3.9) where each age class expressed as a proportion of the lifespan and its corresponding reproductive effort value were calculated and presented in Figure 3-28. The scallops from Sunnyside had higher values than those from New Jersey or St. Andrews, e.g. at the mid-point of its lifespan, a Sunnyside scallop had an effort of 67% whereas New Jersey and St. Andrews scallops had values of 57% and 45% respectively.

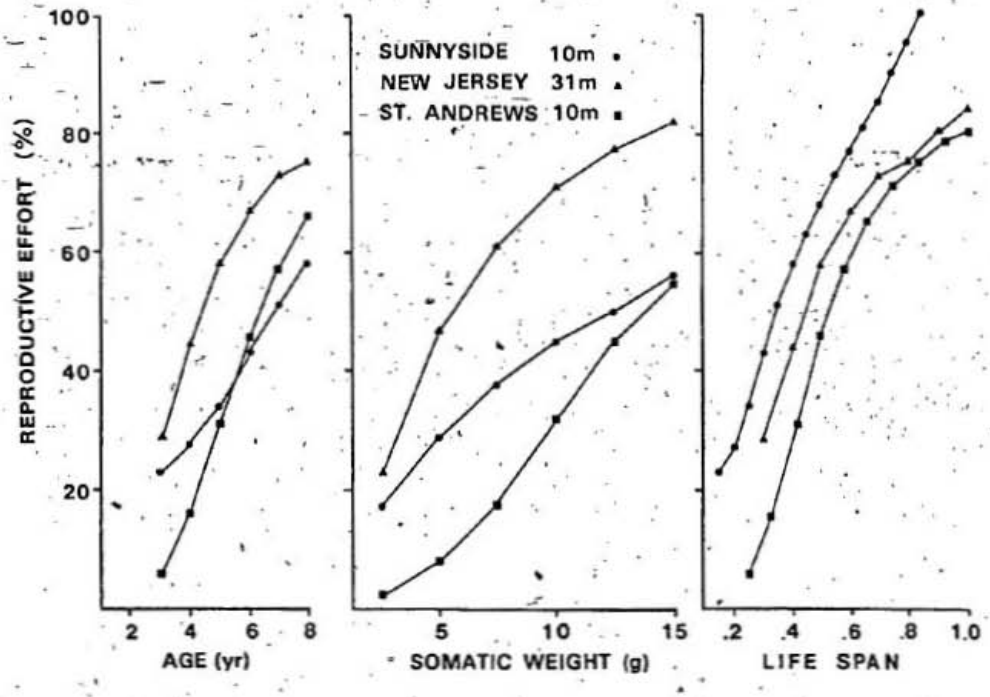


Figure 3-28: Values for age specific reproductive effort, relative weight specific RE and RE for age classes expressed as a proportion of life span for scallops collected in Sunnyside, New Jersey and St. Andrews.

Chapter 4
DISCUSSION

4.1. Growth and Production

The deeper water environments were considered less favourable for scallop growth due to fewer cumulative day degrees and less total available ration to these suspension feeding bivalves. Poorer conditions were reflected in slower shell growth rates for the scallops collected from the deeper water environments. Despite unavoidable errors in assigning ages to individual scallop specimens I have confidence that the age estimates used for calculations were accurate for each depth collection and that meaningful results were obtained. The results of the multiple observer study revealed that at least one of the observers was capable of accurately and consistently determining age from annual rings on the shell and ligament.

The observed differences between shallow water populations, deep water populations and the faster growing cultured scallops became even clearer when the age-specific somatic weights were considered. These results are consistent with observations on *Hinnites multirugosus* by Leighton (1979), and on *Mytilus edulis* by Kautsky (1982b) and Rodhouse et al. (1984), all of whom reported more rapid shell growth and greater tissue weight in bivalves from shallow water than in those from deeper water or growing on the bottom. More rapid tissue and shell growth have also been recorded in mussels (*Choromytilus meridionalis*) collected at lower levels in the intertidal zone than in mussels from more exposed higher areas (Griffiths,1981a,b).

When reproductive output was included in estimates of total production, much greater differences were found between the shallow and deep water scallops and between the cultured scallops and natural populations. The major objective of this work was to investigate the influence of food availability and temperature on growth and production of the scallops by utilizing the gradient which depth provides in the natural environment. This objective was met in that there were good correlations between depth and measured values for food level and temperature, and that differences in these variables were reflected in reduced or enhanced growth and/or reproductive output and in changes in RE. Taking advantage of this natural and to some extent predictable partitioning of the environment has resulted in a study that complements existing and experimental studies in which ration and temperature have been manipulated in the laboratory. A similar result, much greater total production under less environmental stress, has been reported in *Mytilus edulis* by Bayne and Worrall (1980). Subsequently, if more energy was available to grow faster then surpluses may also be available to put into gamete production (Sebens,1982).

Larger maximum heights were observed in scallops from shallower water but the rates at which the animals reached their respective asymptotic shell heights were often similar. Griffiths (1981a) also reported similar k values for growth curves of mussels (*Choromytilus meridionalis*) at different heights on the shore , but greater L_∞ values were found in mussels from the lower zone. Greater maximum sizes have been recorded in suspension feeding sea anemones growing in the more favourable lower tidal zone (Sebens,1982). The cultured scallops from Newfoundland may or may not follow this trend as there are uncertainties regarding their potential longevity. It is possible that the enhanced expenditure of energy on reproduction and growth during the early phase of the lifespan may have reduced the potential maximum size of cultured scallops i.e.. rapid early growth may not be compatible with long life or larger sizes. According to Calow (1979), results of manipulative experiments are difficult to interpret, but if a mutation that enhances reproduction is selected for then a reduction in the

lifespan would be expected. The scallops occurring naturally in favourable environments may have adapted to their habitat by growing at a moderate rate but reaching a greater maximum size. The theoretical models presented by Sebens (1979, 1982) suggest that maximum size may be increased by raising the food input, and in the natural situation this factor may at least be partially responsible in establishing the maximum size that the organism may achieve in any particular environment.

Male and female scallops from identical collection sites and depths had similar somatic growth rates and, with a few exceptions, the same reproductive output. Differences or similarities between males and females in terms of growth and production may depend on the species involved and the location. For example, in the mytilids *Aulacomya ater* and *Choromytilus meridionalis* there were no differences in growth and production between the sexes (Griffiths and King,1979b; Griffiths,1981b), but differences were observed by Sprung (1983) for the mussel *Mytilus edulis* and by Sundet and Lee (1984) for the Iceland scallop *Chlamys islandica*.

Temperature information for the Colinet and St. Andrews sites and the food availability data from Colinet revealed very little difference in environmental conditions with changing water depth at these locations . Forgeron (1959) reported that the water column in sections of the Bay of Fundy may be vertically homogenous in terms of salinity and temperature for most of the year due to intense tidal mixing. In areas where the water column was well mixed, the particulate energy may be continually resuspended and evenly distributed throughout the entire water column. These apparently minimal differences were reflected in similar shell growth rates for scallops within each of these two sites regardless of depth. The greater somatic growth for the deeper population in Colinet was the only discrepancy in the general depth trend and may have been related to local conditions, such as reduced salinity or greater density. The results emphasize the inadequacy of shell morphometric estimates as growth indicators.

Sunnyside and Dildo are both located in Trinity Bay and similarities in shell growth, somatic growth, maximum size and total production were observed for scallops from comparable depths at each site. Slower growth rates, smaller maximum sizes and much lower productivity were characteristic of scallops from Terra Nova National Park (Bonavista Bay) and Colinet (St. Mary's Bay) compared with those from Sunnyside and Dildo, suggesting that TNNP and Colinet were less favourable environments. Considerable differences in growth and production have also been observed in mussels (*Mytilus edulis*) from locations within short distances of one another (Bayne and Worrall,1980; Bayne et al.,1983; Dickie et al.,1984). Temperature conditions at TNNP were similar to those at the Trinity Bay sites, but information on seston was not available for the former and food may not have been as abundant as at the latter site. There appeared to be less particulate energy at the Colinet site but the cumulative day degrees were much greater than those recorded in Trinity Bay. Bayne and Worrall (1980) have described an instance in which production is lower in a population of mussels (*Mytilus edulis*) experiencing a greater number of cumulative day degrees than a neighbouring population. The authors considered the former population to be under nutritive and temperature stress. These findings, and those of my study are inconsistent with the very simplistic general trend of increased growth with warmer temperatures for a species within its ecological range of temperatures (Newell,1979), and there is accumulating evidence to support reexamination of this dogma (for review see Bayne and Newell,1983).

The high temperatures which scallops from Colinet experience may be above the optimum for this species in Newfoundland. High water temperatures could be responsible for an increased metabolic energy expenditure, and when coupled with reduced food availability may decrease growth and maximum size (Sebens,1982). Subsequent reproductive output may then also be reduced.

There was considerable annual variation in the cumulative annual energy

content of seston at any given sample depth, but cumulative day degrees were very similar between years. In general, no differences in age-specific shell growth rates between years were expected or observed. This is probably due in part to the difficulty of detecting a short term change, (i.e. over a one year period) in populations where some individuals are over 20 years old, using relatively insensitive shell morphometric parameters. Dickie et al. (1984) reported no year to year variation in shell growth in *Mytilus edulis*. There were however, some indications that the younger scallops from shallower depths at a more favourable site such as Sunnyside may be capable of shell growth spurts under suitable conditions.

The production of somatic tissue was not variable between years and age-specific somatic growth rates were equal in each year for a given population. The regression equations for somatic weight versus shell height were occasionally different between years but the absolute differences in mean weight were not very great .

Gamete production (Pr) was frequently variable from year to year, especially in those scallops from the shallower depths at the more favourable sites. Further evidence of greater variation in reproductive output than in somatic growth was demonstrated by the regression equations for Sunnyside scallops (10m) from 1981-83, e.g. the somatic weight versus shell height regressions consistently had r^2 values of 0.97 (Table A-18), whereas the prespawned gonad weight versus shell height regressions for the same specimens had r^2 values between 0.73 and 0.87 (Table A-24). Annual variation in fecundity was reported by Thompson (1977) for *Placopecten magellanicus* in Newfoundland in 1973 and 1974 and for mussels by Thompson (1979), Griffiths (1981b) and Bayne et al. (1983). Environmental conditions for scallop production in 1982 were apparently more favourable than in 1981 or 1983 in some areas of Newfoundland. The greater production of gametes observed in 1982 at 10m in Sunnyside was associated with greater food availability in that year, compared with lower ration conditions and

lower productivity in 1983. The lower summer temperatures before spawning at Sunnyside in 1982 may have also contributed to an increased reproductive output by reducing the energy expenditure required by the animals for maintenance. In addition, scallops from both 10m and 31m in Sunnyside possessed larger and heavier eggs in 1982 than those obtained in 1983 from scallops at the same depths.

The environment which scallops experience in Newfoundland is unpredictable, and it may be an appropriate reproductive strategy to invest any surplus energy available into gametes when more favourable conditions are encountered. This may be advantageous in that it may not be possible for the animal to support a larger body mass in that particular environment in subsequent years had the extra energy been invested in somatic growth. In 1983 the conditions at 31m in Sunnyside appeared to be more favourable in terms of food availability than in 1982, yet a large increase in gamete production was not observed as these smaller more stressed scallops from 31m may lack the capability to divert any excess energy into gametes, as observed in the population from 10m. There are also probable qualitative differences in ration between depths and sites (e.g. fatty acids, amino acids) which lay outside the scope of this study but may contribute to variation between populations in growth and gamete production.

When the shell heights for populations from Sunnyside, St. Andrews and New Jersey were fitted to the Von Bertalanffy growth equation, the parameters generally followed the predicted trend of lower growth rates (k) but greater longevity and larger maximum sizes (H_∞) in the northern populations. Despite many more cumulative day degrees in New Jersey and St. Andrews than in Newfoundland, scallops from all three had the same absolute growth rates, at least until age eight. This indicated that the only real difference between the three populations was the maximum size that the scallops attained, and since the Newfoundland scallops grew larger their relative rate of growth or k value was reduced. This demonstrates that comparisons of k values between populations

with different L_∞ values (or vice versa) may be inappropriate and that comparisons of absolute growth would be better than simply using the parameters of the Von Bertalanffy equation.

A correction for cumulative day degrees described by Ursin (1963) was applied to the shell growth equations for Sunnyside (10m and 31m), St. Andrews and New Jersey populations and the data presented as growth per 1000 D° in Table 4-1. As the relationship changes with age (Thompson, 1984a) values for several age classes plus estimates of production per 1000 D° are also included in the table. After correction for temperature the deep water population had faster shell growth than the shallow water population and both of these grew much more rapidly than the more southerly St. Andrews and New Jersey populations. However, when total production estimates were adjusted for temperature the shallow population was relatively more productive, followed by the 31m population in Sunnyside. Once again, estimates for the two more southerly populations were the lowest. Similar observations of relatively fast shell growth per 1000 D° for other populations of northern bivalves has also been presented by Hickman (1979) and Thompson (1984a). The results of this geographical study and conclusions presented by Thompson (1984a) suggest that northern populations are not necessarily growing more slowly or are less productive merely because the water is cooler, in contrast to previous studies of shell growth based only on the parameters of the Von Bertalanffy equation. Local variation in conditions may greatly influence growth and production, and before using one population to characterize an entire geographical area it is desirable to obtain information on natural variation to determine if the population to be considered is typical of the area.

In a similar way, total production was also expressed per unit of food available (kJ/1000 DJ l^{-1}) in 10m and 31m at Sunnyside (Table 4-2). The influence of temperature and food supply on growth and production in several molluscan groups has been reviewed by Bayne and Newell (1983). Several of

Table 4-1: Annual increments in shell growth and total production for scallop populations from Sunnyside, New Jersey and St. Andrews. Cumulative day degrees are presented in brackets beside each depth in the table headings. Values in brackets in the body of the table are ⊿mm and ⊿kJ per 1000D°.

	Sunnyside				St. Andrews		New Jersey	
	10m(1451)		31m(957)		10m(2536)		31m(3180)	
$k\Delta$	1.3×10^{-4}		1.7×10^{-4}		7.9×10^{-5}		5.0×10^{-5}	
$D\Delta$	797.5		95.7		1040		350	
Age	(mm)		(mm)		(mm)		(mm)	
3	22.8	(15.7)	17.4	(18.2)	22.1	(8.7)	19.9	(6.3)
5	15.8	(10.9)	12.6	(13.2)	14.7	(5.8)	14.4	(4.5)
7	10.8	(7.4)	9.1	(9.5)	9.9	(3.9)	10.4	(3.3)
12	4.4	(3.0)	4.1	(4.3)				
18	1.4	(1.0)	1.6	(1.7)				

Total Production (1983)

	(kJ)		(kJ)		(kJ)		(kJ)	
3	50	(35)	35	(37)	55	(22)	48	(15)
5	124	(86)	61	(64)	98	(39)	118	(37)
7	153	(105)	70	(73)	155	(61)	223	(70)
12	198	(137)	80	(84)				
18	184	(127)	61	(64)				

Table 4-2: Total production expressed per 1000 DJ l^{-1} available food and per 1000D° for scallops from 10m and 31m at Sunnyside. The mean differences between these derived quantities (in percent) for the two populations are also included.

	Pt (kJ/yr) (uncorrected)			Temperature (kJ/1000D°)			Food (Pt kJ/1000 DJl^{-1})			Factor(f) =TxFood (Pt DJ/f)		
Age	10m	31m	%	10m	31m	%	10m	31m	%	10m	31m	%
3	50	35	30	35	37	-6	6	5	13	4	6	-24
5	124	61	51	86	64	25	16	9	39	11	10	8
7	153	70	64	105	73	31	19	11	43	13	11	14
12	198	80	60	137	84	39	25	12	50	17	13	24
18	184	61	66	127	64	50	23	9	59	16	10	38
	$\bar{X}$= 54%			$\bar{X}$= 28%			$\bar{X}$= 41%			$\bar{X}$= 12%		

		Cumulative D°	Cumulative Food(DJ/l)	Interaction Factor
Sunnyside	10m	1451	8004	11.61×10^6
	31m	957	6474	6.20×10^6

these studies and other published reports too numerous to cite here have indicated that temperature and food, or both, are responsible for observed differences in growth and production. Owing to the probability that these two factors interact in this context, a factor to take this into account was calculated by multiplying cumulative day degrees by cumulative day Joules per litre (Table 4-2). A 10m scallop was 54% more productive than one from 31m when temperature and food availability were not taken into account, but 41% greater when corrected for food availability and only about 28% greater after correcting for temperature. The greater apparent influence of temperature was simply due to a greater differential

(i.e. temperature was 1.5 times greater in 10m than at 31m but food availability was only 1.2 times greater) and did not indicate that it was the factor most responsible for the observed differences. The small difference observed (12%) when both temperature and food were considered simultaneously should not be interpreted as a rigorous, quantitative measure of the relative contributions of the two factors to variation in production, but rather to suggest that they interact, although it is difficult to partition the variance when the relationship between them is presently unknown and likely to be variable.

4.2. Gametogenic Cycles

Less favourable conditions in the deeper water environments were not only reflected in less somatic and gamete production for the scallops collected there, but also influenced the rates of gamete development and maturation. Shallow water scallops were characterized by more rapid gametogenesis after spawning, and by a greater GVF for total gametes (apart from the periods immediately before and after gamete release). Rapid maturation of gametes in both deep and shallow populations in Newfoundland occurred immediately after the spring bloom. Kautsky (1982b) described a similar rapid maturation after the spring bloom for *Mytilus edulis* in the Baltic Sea. Spawning took place at approximately the same time in both the deep and shallow populations of *Placopecten magellanicus* in Newfoundland. Skreslet and Brun (1969) also reported similar spawning times for shallow (20m) and deep water (50m) populations of the scallop *Chlamys islandica*, despite greater gonadosomatic indices recorded for the shallow populations.

According to Bayne and Newell (1983), certain reproductive characteristics of a species, e.g. mean egg size, the energetic cost of producing a unit of gametes, the relationship between egg production and body size and an increasing reproductive effort with increasing body size, may all remain unchanged over a wide range of environmental conditions. In contrast, the timing of gametogenesis and spawning, fecundity and maximum reproductive effort are more likely to vary

in relation to environmental factors. Differences observed between the deep and shallow populations at Sunnyside appeared to be consistent for both the more conservative and the variable characteristics. For example, the mean egg size was identical in both populations, although it may not be possible to generalize, since Bayne et al. (1978) reported smaller eggs for laboratory stressed *Mytilus edulis* and Barber and Blake (1983) observed much smaller eggs in bay scallops (*Aequipecten [=Argopecten] irradians*) from Florida than in those from Massachusetts. Furthermore, some annual variation in egg size was observed in *Placopecten magellanicus* during my study. More variable reproductive characteristics, such as fecundity and rate of gamete development, were considerably reduced in scallops from deeper water, where conditions were less favourable. However, the timing of spawning and the maximum reproductive effort attained in each environment appeared to be similar, although when reproductive effort data expressed as a proportion of ingestion were compared, maximum values were higher in the shallow population.

Intraspecific differences in reproductive characteristics of several bivalves have been described for populations occurring under a variety of environmental conditions or degrees of stress. For example, there may be lower values for gonad indices or GVF values (Skreslet and Brun,1969; Newell et al.,1982; Rodhouse et al.,1984) and less synchronous spawning (Lowe et al., 1982; Newell et al., 1982) for populations from less favourable environments. Examples of dual spawnings and subsequently greater reproductive output in populations which experience good conditions of food availability and temperature have also been reported (Bayne and Worrall,1980; Rodhouse et al.,1984) and, conversely, loss of dual spawning in a population of *Mytilus edulis* subjected to natural thermal stress for two consecutive years has been reported by Lowe et al. (1982). Nichols and Barker (1984) presented evidence of reduced fecundities , lower gonad indices and less synchronous spawning in populations of the starfish *Asterias rubens* collected from an impoverished subtidal site, compared with those from a nutritionally more favourable intertidal site. Variations in these more flexible reproductive

characteristics may be good predictors of anthropogenic and natural stress (Bayne,1983).

Inhibition of gamete development by low temperatures and poor rations in the bay scallop *Aequipecten (=Argopecten) irradians* has been documented by Sastry (1966) and Sastry and Blake (1971), and in *Perna perna* by Velez and Epifanio (1981). Low temperatures are unlikely to be the cause of slower gamete development in specimens of *Placopecten magellanicus* from 31m than in those from 10m, because from approximately November to May temperatures were identical in both depths in every year, but they may influence maturation because temperatures at 10m were consistently higher than at 31m during the summer months. Neither is it clear whether ration influences the rate of gametogenesis, because in 1983 the annual cumulative day joules per litre were similar in 10m and 31m, but the deeper scallops still lagged behind in terms of gamete development and maturation and in GVF for total gametes. This may be related to the fact that a major proportion of the annual cumulative day joules per litre for this depth was available during two weeks of the bloom and for four weeks after the bloom, i.e. 25 to 30% of the annual ration was presented over a six week period when temperatures were low, whereas reduced levels were observed for the rest of the year. It may be that scallops are sometimes exposed to very high concentrations of food, such that they can not take full advantage of the available ration. In contrast, the scallops from 10m received less than 20% of their annual budget during the same six weeks and occasionally experienced periods of relatively high food concentrations during late summer and autumn when temperatures were warm, i.e. their annual food budget was more evenly spread over the entire year rather than concentrated into one short period.

Gamete volume fraction values for total gametes were significantly greater for males than females, except immediately before and after spawning, in both the shallow and deep water scallops. More rapid rates of gamete development for males in several species of bivalves have also been reported by Seed (1976), Newell

and Bayne (1980), Newell et al. (1982) and Sundet and Lee (1984). Sundet and Lee (1984) also recorded seasonal differences in gonad wet weights with higher values for males, which they attributed to an apparently different energetic cost of producing sperm and eggs. There were no consistent indications of significantly heavier male gonads in this study on *Placopecten magellanicus*, and Shafee and Lucas (1980) found no significant differences in somatic or gonad dry weights between male and female *Chlamys varia*.

Distinct differences were observed in the annual cycle of gametogenesis and the timing of spawning between the New Jersey and Sunnyside populations. General trends of earlier seasonal spawning in more southerly mytilid populations have been presented by Seed (1976), but in other bivalves, e.g. the bay scallop *Argopecten irradians*, spawning may be later in more southerly latitudes (Sastry,1970; Barber and Blake,1983). Scallops from Newfoundland spawned in late August or early September, whereas the New Jersey population spawned during early to mid-October which seems consistent with the trend in the bay scallop, but if the partial spawning in the New Jersey population is taken into consideration the pattern becomes less straightforward. A review of spawning periods for *Placopecten magellanicus* (MacKenzie,1979) has revealed a complex situation which cannot be interpreted in terms of temperature alone. For example, scallops from North Carolina and Virginia spawn in July, northern scallop populations apparently spawn between June to September and those from Georges Bank spawn between September and October. While water temperature has been well correlated with reproductive cycles and has often been considered to be the major factor in their control, recent, thorough studies have emphasized the importance of local conditions. Thus Newell et al. (1982) demonstrated that the greatest difference in reproductive cycles of *Mytilus edulis* from latitudinally separated populations on the east coast of the U.S. was between two populations on Long Island, N.Y., which experience near identical temperature cycles but differing regimes of food availability.

4.3. Physiological Measurements

Clearance rates and oxygen consumption rates were determined for both shallow and deep water populations at their respective ambient temperatures to gain insight into energy acquisition and expenditure by the scallops. Observed differences may not be directly comparable except during the months when ambient temperatures were similar. Water temperatures were the same during January to April/May and no differences were observed in VO_2 between populations, but clearance rates were generally higher in the 31m population. Water temperatures were higher between May and November and significantly higher metabolic rates were recorded for the 10m scallops, yet despite the lower temperatures clearance rates for the 31m scallops were at least equal to or greater than those of the 10m scallops. The GVF for total gametes was higher in the 10m scallops, except immediately before and after spawning.

Correlations between oxygen consumption and gametogenic cycles in bivalves may be a function of the specific environmental conditions in which the animals occur. For example, Thompson (1984b) found no clear relationship between VO_2 and the gametogenic cycle for *Mytilus edulis* in Newfoundland, whereas Widdows and Bayne (1971) and Gabbott and Bayne (1973) recorded high VO_2 values for the same species subjected to low winter temperatures in the North Sea and attributed this to the cost of gametogenesis. Positive correlations between gametogenic activity and VO_2 for *M. edulis* and *Cardium edule* were reported by Bayne and Widdows (1978) and Newell and Bayne (1980) respectively. The relationships between environmental and physiological variables in this study have been presented as a correlation matrix in Table 4-3. The lack of relationship between VO_2 and GVF in this study was similar to the results of Thompson's (1984b) study on *M. edulis* from Newfoundland.

Oxygen consumption was strongly correlated with temperature in *Mytilus edulis* (Thompson,1984b), in three populations of *Scrobicularia plana* (Worrall et al.,1983) and in the 10m *Placopecten magellanicus* population monitored in this

Table 4-3: Matrix of Spearman correlation coefficients for environmental and physiological variables where SWT is the somatic weight of a standard 140 mm scallop.

10m

	FOOD	CR	VO_2	GVF	SWT	TEMP
FOOD	-	0.321	0.669*	0.710*	-0.253	0.212
CR		-	0.879**	-0.131	-0.148	0.970***
VO_2			-	0.284	-0.241	0.806**
GVF				-	-0.284	-0.230
SWT					-	-0.091
TEMP						-

31m

FOOD	-	0.683*	0.643*	0.476	-0.571	0.192
CR		-	0.922***	-0.036	-0.192	0.657*
VO_2			-	0.092	-0.262	0.383
GVF				-	-0.619*	-0.371
SWT					-	0.012
TEMP						-

study. There was no correlation, however, between VO_2 and temperature in the 31m population or for a population of *Mytilus edulis* in a Devon estuary (Bayne and Widdows,1978), and Newell and Bayne (1980) recorded similar findings in *Cardium edule*, which they attributed to the cockle's ability to acclimate metabolic rate to temperature changes. Vahl (1978) found that temperature changes did not greatly influence the seasonal metabolic rates of *Chlamys islandica*, but that a major portion of the seasonal variability was explained by food availability. Food availability was also positively correlated with VO_2 for both scallop populations in this study, and was almost significant for a population of *M. edulis* from Newfoundland (Thompson,1984b). Food availability was also

well correlated with GVF in one population (10m) and CR in the other (31m), suggesting a relationship, although not completely clear, between enhanced food levels, clearance rates and the increasing energy demands of gametogenesis.

Clearance rates were positively correlated with temperature and VO_2 in both populations suggesting that the scallops increase their feeding rates in response to enhanced metabolic expenditure associated with warmer ambient temperature. However, no seasonal patterns of CR were observed for *Mytilus edulis* from Newfoundland (Thompson, 1984b). The mean monthly somatic weight of a standard sized animal was not correlated with any other variable, excepting a negative relationship between somatic weight and GVF in the 31m population only. This suggested that as gametogenesis proceeded body weight generally declined, and that after spawning the somatic weight increased again, i.e. in the more stressed population gametogenesis may have been making demands on the somatic tissue.

No seasonal variation in the exponent of the allometric equation relating clearance rates or VO_2 to dry weight was observed for either population in this study, although there were significant differences in intercepts. The common slope value of 0.70 for the clearance rate of *Placopecten magellanicus* is well within the range described for other pectinids, e.g. 0.60 for *Chlamys islandica* (Vahl, unpublished, cited in Bayne and Newell,1983), 0.58 for *Argopecten irradians* (Kirby-Smith,1972) and 0.82 for *Pecten irradians* (Chipman and Hopkins,1954). The common slope of 0.89 for oxygen consumption was comparable to the value of 0.81 recorded for *Patinopecten yessoensis* (Fuji and Hashizume,1974) and the range of 0.75 to 0.93 recorded for *C. islandica* (Vahl,1978).

Despite great seasonal fluctuations in the energy content of the seston from all water depths, the range of total particulates was consistently between five and 10 mg l^{-1} except during the bloom, when levels up to 16 mg l^{-1} were recorded. The organic content was consistently between 15 and 30% of the total

particulates and no production of pseudofaeces by scallops was observed during this study. Thompson (unpubl.) has rarely observed pseudofaeces production in *Placopecten magellanicus* or *Mytilus edulis* feeding on natural particulates in Newfoundland, and similar results have been reported for *Cardium edule* (Newell and Bayne,1980).

The production of pseudofaeces in bivalves is apparently not only related to the concentration of suspended material but also to its nature (Foster-Smith,1975). For example, Widdows et al. (1979) reported pseudofaeces production in *Mytilus edulis* at relatively low concentrations (< five mg l^{-1}) and considered that large amounts of silt (75-95% of the total seston) in the total seston were diluting the food supply, as some algal material present was being removed with the pseudofaeces, resulting in a reduced ingestion of organic material. Widdows et al. (1979) found no evidence of preferential selection of organic over inorganic particles, but Newell and Jordan (1983) observed preferential ingestion of organics and rejection of inorganic material as pseudofaeces in *Crassostrea virginica* fed on artificial and natural diets with particulate loads less than five mg l^{-1}. Preferential selection (Kiorboe and Mohlenberg,1981) and the enhancement of absorption efficiencies as a result of adding suspended bottom material (Mohlenberg and Kiorboe,1981) to artificial diets have also been described for bivalves. According to Newell and Jordan (1983), unless pseudofaeces production and preferential selection can be demonstrated at naturally low seston levels the significance of such a mechanism may not be ecologically meaningful. Robinson et al. (1984), working with the surf clam *Spisula solidissima*, obtained similar results to those of Widdows et al. (1979) on *Mytilus edulis* i.e., as turbidity increased there was an increase in the amount of algae in the pseudofaeces and a subsequent decrease in ingested ration. The levels reported by Robinson et al. (1984) were admittedly higher than those encountered naturally by *S. solidissima* except near major anthropogenic inputs.

4.4: Reproductive Effort, Value and Cost

One major cornerstone of modern life history theory is the assumption that current reproduction will have a deleterious effect on future reproduction. This is related to the concept that food resources are always limiting and enhanced investment in any one process must reduce the allotment of energy for others, i.e. there is a tradeoff between metabolic processes of reproduction and growth, resulting in reduced fecundity, survival and fitness (Calow,1984). Without a clear cost function related to reproduction, selection would favour maximization of reproduction and survival rather than optimization of reproductive effort and reproductive value as predicted by theory (Bell,1984a).

The underlying tenets of the so-called "optimization theory" have been challenged by Tuomi et al. (1983), who have also provided alternative concepts for selection and reproductive cost. Tuomi et al. (1983) suggested that selection may be influencing the whole organism rather than separate traits, and strategies may not necessarily be optimized but instead be a result of the elimination of unfit characteristics. Reproduction may not necessarily result in a cost function because increases in energy may result from more efficient conversion of available resources or simply by increasing ration, which may uncouple somatic costs from the influence of reproduction (Tuomi et al.,1983). Bell (1984a) reevaluated the evidence relating to the cost hypothesis and concluded that it had relatively weak empirical support. In a series of experiments by Bell (1983,1984a,b,), the relationship between present reproduction and future reproduction indicated a positive trend rather than negative, from which he concluded that further rigorous testing should be undertaken, especially when considering the possible effects of variable egg size on survival. The lack of data for components of the optimization theory such as reproductive effort or residual reproductive value may be due to our lack of ability to measure them accurately rather than a deficiency of the theory itself (Thompson,1984a).

An understanding of how phenotypic properties vary in relation to factors

such as age, development and physiological condition is necessary before the overall consequences of a particular reproductive pattern to the organism may be evaluated (Bayne,1984; Stearns,1984). Stearns (1984) emphasized caution when interpreting predictions that are realized under certain circumstances, as they may not necessarily hold true for a variety of conditions. A considerable body of literature is rapidly accumulating on reproductive patterns in marine bivalves, especially *Mytilus edulis*, in which fecundity and reproductive effort have been shown to vary in response to changing environmental conditions (Bayne et al.,1983). Bayne (1984) demonstrated that small mussels have advantages in energy acquisition and expenditure up to an "optimal" size that may enable them to reproduce without diverting energy away from somatic growth, i.e. there is no cost component in the small individuals. Above this optimum size, however, a cost function results and reproduction takes place at the expense of somatic growth. Hawkins (1983) and Shafee and Lucas (1980) both describe dual spawning cycles composed of one major spawning period fueled by energy reserves, high RE and reckless behaviour and a secondary restrained spawning period for *M. edulis* and *Chlamys varia*, respectively. If this situation is generally applicable then the associated risk of this *reckless* spawning period to the adult may be justified if the period of growth and development of the larva corresponds to favourable environmental conditions such as the spring bloom and good growth conditions associated with the summer months (Bayne,1984). This cost, related to high reproductive effort, may be beneficial to the young and positively correlated with fitness by achieving a good return for a well timed investment.

The proportion of energy allocated to reproduction (RE), expressed as a proportion of total production and as a ratio of ingested ration, increased as *Placopecten magellanicus* grew larger and older and eventually exceeded 100% of net production, due to somatic degrowth. Comparative estimates of fecundity or reproductive effort for various populations of *P. magellanicus* are unavailable as most of the ecological energetics and life history theory in bivalves is mainly

confined to *Mytilus edulis* and to *Chlamys spp.*. Increasing RE with size and age has been reported for several bivalve species including *Mytilus edulis* (Bayne and Worrall,1980; Kautsky,1982b; Bayne et al.,1983; Thompson,1984a) and two species of pectinids, *Chlamys islandica* (Vahl,1981a) and *Chlamys varia* (Shafee and Lucas,1982). Vahl (1981b) reported that growth is probably negative in scallops greater than 20 years of age, and degrowth in freshwater triclads has also been reported (Calow,1979). Increasing RE with age seen in this study was consistent with predictions by Charlesworth and Leon (1976) that RE should be an increasing function of age for species with low mortality in the reproductive period and where growth continues after maturation.

Age specific RE was consistently higher in the Sunnyside 10m population compared with deeper populations from the same site and with Colinet populations, which have apparently been subjected to a more severe degree of environmental stress. In order to assess the consequences of a particular level of effort it is necessary to quantify the available food source (Haukioja and Hakala,1978; Hirshfield,1980) in addition to the actual ingested ration (Calow,1979). When these factors were considered, the shallow populations still had higher RE as a proportion of ingested ration and a greater effort when food availability was similar than had the deeper populations. Lower RE associated with higher stress levels were also observed in *Mytilus edulis* populations (Bayne et al.,1983). After standardization for shell growth rate, higher levels of RE were still characteristic of populations experiencing more favourable conditions (Bayne et al.,1983), and the same result was observed in this study after standardization for body weight. The natural stress associated with wave action and competition also reduced RE for a starfish population in a relatively harsh environment, but was reversible when the population was transplanted to a more favourable environment (Menge,1974). All these results are consistent with predictions by Goodman (1979) that RE should increase under more favourable conditions. Nevertheless, inconsistencies have been reported in a number of species subjected to experimental conditions of stress such as reduced ration (Calow and

Woollhead,1977; Bayne et al.,1978; Hirshfield, 1980; Thompson,1983) where RE actually increased at the expense of somatic growth, despite reduced fecundity demonstrated in some of the studies. The apparent discrepancies may be explained by "the nature of the experimental regimes, which usually represent abrupt, unpredictable changes in conditions that may not elicit the same response from the animal as a consistently poor environment, in which there is the opportunity for long term adaptation to occur" (Thompson,1984a p. 255).

Greater values for age specific RE were characteristic of cultured scallops, which is again consistent with theory, as the conditions associated with suspended culture were assumed to be more favourable due to faster growth and greater production by the animals. The conditions for suspended *Mytilus edulis* have been shown to be superior to those in their natural habitat (Rodhouse et al.,1984). After standardization for the more rapid growth of cultured scallops, and by presenting RE values for each age class expressed as a proportion of expected lifespan, higher values were observed for the naturally grown scallops. This second estimate indicated that the naturally grown scallops switched the emphasis from somatic growth to reproductive output (i.e. RE>50%) at the same age as cultured animals, but at an earlier stage relative to longevity. It is difficult to establish whether or not there are consequences resulting from delay in switching from growth to reproduction in the cultured scallops, as the reproductive patterns observed under the experimental conditions of suspended culture have been established over a short period and may not be generally applicable to future generations. Theoretical implications of particular reproductive strategies on the longevity of a species are of little interest to commercial culturists, who are primarily concerned with total yields and growth rates. According to this study the cultured scallops should reach marketable size in approximately three years, compared with the four or five years required for natural populations, depending on local conditions. The commercial culture of scallops would be more efficient if markets existed for scallop gonads as in Japan (Ventilla,1982), especially considering the much greater age specific total production of the cultured scallops and the fact that the gonad may comprise >50% of total wet weight.

The age specific RE values and the relative effort for scallops of standard weight were both higher in the New Jersey population compared with those scallops collected from St. Andrews and Sunnyside. This is attributable to greater reproductive output, lower somatic production at given age and the fact that New Jersey scallops of given weight are physiologically older than a scallop with the same absolute age from a northern population. For example, an eight year old in New Jersey may only live two more years whereas a scallop of the same age in Sunnyside may live for another 12 years or more. No latitudinal trends were apparent, and between population comparisons of RE differed according to which of the two indices was used, although the St. Andrews population consistently showed the lowest values for RE for both indices, and higher values were observed in the Sunnyside population when longevity was taken into account. The relatively early switch from somatic growth to gamete production and the higher level of RE in Sunnyside scallops may be functions of the much cooler environment, lower mortalities and high probability that the scallops will ultimately attain the maximum size ,i.e. early emphasis on reproduction will not necessarily be reflected in a reduction in maximum size.

Variability in estimates of fecundity obtained for populations sampled in different years does not necessarily mean that reproductive effort changed, although the two quantities are often mistakenly considered synonymous (Thompson,1979). In studies on species from fluctuating, unpredictable environments it is necessary to consider the possibility that the organism has the potential to vary its reproductive pattern accordingly, or misleading conclusions may result (Nichols,1976). In addition to variable reproductive effort between populations from different environments, annual variation in RE for the same population in different years was also recorded for some populations in this study of *Placopecten magellanicus* and for other bivalve species (Haukioja and Hakala,1978; Shafee and Lucas,1982; Bayne et al., 1983). When annual differences in RE were observed in this study they were usually greatest in 1982 when available ration was better, at least for the shallow Sunnyside populations.

However, improved conditions of food supply are not necessarily reflected in significantly higher fecundity or RE, as evidenced by the 31m population from Sunnyside in 1983 compared with 1982. The extra energy available in 1982 for the shallow population was all invested in gametes, as no annual differences in somatic growth were observed. According to Spight and Emlen (1976), this unconstrained type of reproductive strategy or ability is advantageous because it is not necessary to grow in order to increase reproductive output. There are also advantages to devoting more energy into reproduction during good years because this will presumably place less demand on somatic growth and maintenance (Ballinger,1977).

Reproductive value and residual reproductive value were much higher in scallops from shallow water than in those from deep water. Steadily increasing reproductive values and residual reproductive values which increased to a maximum before declining with advancing age were observed in this study and in other bivalves by Vahl (1981a), Bayne et al. (1983) and Thompson (1984a). Brody et al. (1983) have emphasized that investment in growth also contributes to RRV as a result of increased fecundity, and Haukioja and Hakala (1978) and Tuomi et al. (1983) consider that it is impossible to determine the contribution of somatic growth to reproduction in species where fecundity is well correlated with size. Identical age-specific mortality rates were used to calculate RRV for both the deep and shallow water populations, despite the possibility that faster growing populations may have greater mortality (Craig and Kipling,1983). The mortality estimates obtained in this study were considered superior to those previously obtained for sublittoral species such as scallops. This is because mortality was directly monitored in this study, providing age specific rates rather than a single population value obtained from such indirect means as dredging or size frequency distributions. Dickie et al. (1984) concluded that whereas environmental factors at different locations influenced growth of *Mytilus edulis*, a phenomenon observed in this study for *Placopecten magellanicus*, mortality patterns were influenced more by the genetic component of the stock. The deep and shallow

water populations of *P. magellanicus* from this study are only separated by 100m-150 m, and it seems unlikely that a species such as this, with a planktotrophic larval stage and some mobility in the years following metamorphosis, would diverge genetically along a small vertical gradient. On the other hand the faster rate of growth may be advantageous in reducing mortality by enabling *P. magellanicus* to attain a threshold size, rendering them less susceptible to predation (Elner and Jamieson,1979; Jamieson et al.,1982), or to withstand better unpredictable periods of stress for longer periods if and when such conditions occur in the shallow environment. Paine (1976) and Seed and Brown (1978) have presented evidence that growth may provide a means of escaping predation for *Mytilus californianus* and *Modiolus modiolus*, respectively. Owing to the much lower fecundity of the deeper populations, similar RRV values to those of the shallow populations could only be achieved if scallops from 31m lived much longer or had much lower mortalities than those from 10m. Therefore the difference between these two populations is real (i.e. not an artifact of mortality rates) but the magnitude of the difference may be variable.

According to predictions of the optimization theory presented by Goodman (1982), the maximum value of RRV should correspond approximately to the age of maximum growth. The results of this study and those for *Mytilus edulis* by Bayne et al. (1983) and Thompson (1984a) were consistent with theory, although Vahl (1981a) described a different relationship in *Chlamys islandica*. Maximum growth in the Icelandic scallop occurred at age six (Vahl,1981b) but maximum RRV was observed at age 13 (Vahl,1981a), which corresponded with the age at which seasonal degrowth was first recorded (Vahl,1981b). Like *C.islandica*, *P. magellanicus* also had a longevity of 20+ years, with maximum growth rate near age six, but its maximum RRV occurred much earlier, at approximately four years. Nothing is known about seasonal degrowth in *P. magellanicus* from this study, but annual degrowth (by which the somatic tissue shrinks at the end of the year and does not appear to regain the somatic energy) was not observed until age

16 or 17. When the ages at which maximum growth and maximum RRV occur in these species of bivalves were expressed as a proportion of the expected lifespan, some interesting trends emerged. For example, the maximum growth rates for mytilids ranging in age from eight to 12 years took place at about four to six years, roughly the half way point in the life span (Bayne and Worrall,1980; Thompson,1984a), whereas maximum Pg for pectinids living more than 20 years was also around age six (Vahl,1981b), which corresponds approximately to 30% of life span. Maximum RRV for the Newfoundland populations (Thompson,1984a; and this study) were at ages roughly corresponding to 33% and 20% of the lifespan respectively, but the maximum RRV values for mussels (Bayne et al., 1983) and Icelandic scallops (Vahl,1981a) from other geographical areas corresponded to ages representing approximately 50% and 65% of the lifespan respectively. These differences may be attributable in part to the U-shaped mortality curves used in the Newfoundland studies and the constant rates of mortality used in the other two studies.

Increasing RE with age was reflected in a corresponding increase in the cost index. The shallow population displayed unconstrained reproduction and consistently higher RE regardless of the food availability and consequently displayed higher indices of cost. Positive values for cost were not observed for the deep population and in general *Placopecten magellanicus* from Newfoundland may be considered restrained in terms of reproductive strategy. Similar conclusions, namely that reproductive behaviour in bivalves is generally restrained but may be reckless under certain conditions, have been presented by Shafee and Lucas (1980), Bayne et al. (1983), Hawkins (1983) and Thompson (1984a). Despite the restrained behaviour of the giant scallop suggested by the index of reproductive cost, real costs are noticeable in scallop populations from almost every site in Newfoundland. For example, somatic tissue weight declined after age 16 or 17 but reproduction still proceeded, presumably at the expense of the soma. This is consistent with Bayne's (1984) concept that a cost function may only exist in bivalves after an optimum size is surpassed.

The shallow populations, unlike the deep populations, grew under more favourable environmental conditions but were also able to maximize better their energy gain from feeding, a capability which may be considered a good fitness correlate (Calow,1982). As an animal's fitness may be evaluated by the number of surviving offspring produced during its lifetime (Hirshfield,1980), the shallow water scallop populations have much greater fitness. The problem of interpreting egg size and survival, raised by Bell (1983), is not really applicable in this study because the harsh natural conditions associated with the deeper water environment resulted in lower fecundities but not smaller eggs. Thus the eggs from both depths would presumably have equal chances of survival and the shallow populations are more fit by virtue of their greater fecundity. Furthermore, a reduction in fitness from the optimum may occur when the physiological compensatory mechanisms that the animal possesses are not completely efficient under poor conditions, resulting in less available energy (Bayne,1983).

4.5. Conclusions

1. Shallow water environments were more favourable for growth and reproduction of scallops than deep water locations, owing to the greater food availability and more cumulative day degrees in the former.

2. Variable local conditions also influenced scallop growth and production estimates, as large differences were observed between populations collected from four different bays in Newfoundland.

3. Shell growth was the least sensitive predictor of environmental conditions as relatively small differences or no differences at all were

observed between populations at various locations. Somatic weight was more sensitive to environmental factors, and there were much greater inter-population differences in somatic weight than in shell height, although neither quantity varied from year to year.

4. Reproductive output varied not only between populations from different areas but also between consecutive years in a given population. This suggested that gamete production was strongly influenced by environmental conditions and that annual variation in total production estimates for Newfoundland scallops was primarily due to variation in fecundity.

5. Other reproductive traits such as the rate of gamete development or maturation and reproductive effort were reduced under less favourable environmental conditions. The timing of spawning for populations in Newfoundland appeared unaffected by stressful conditions, but there were differences on a geographical scale. The influence of temperature and food on egg size was somewhat more complex. The strong influence of local conditions prohibits the establishment of general geographical trends based on single measurements such as time of spawning or temperature cycles.

6. Evidence from the physiological studies indicated that the greater growth, reproductive output and resulting improved fitness of the

shallower population was reflected in an elevated metabolic demand and relatively higher estimates of reproductive cost, compared with the deep water populations, despite the overall conclusion that *Placopecten magellanicus* from Newfoundland was generally restrained in its reproductive behaviour. Physiological variables such as CR and VO_2 varied seasonally in relation to ambient temperature and food conditions, all of which appeared to be interrelated in a complex fashion with the energetic demands of gametogenesis.

7. Comparisons of absolute growth rates and production estimates suggest that northern populations of bivalves may not be slower growing or less productive than comparable species from more southerly locations. Again, the importance of local conditions cannot be overstated, and the Newfoundland populations of *Placopecten magellanicus* investigated in this study may not be typical of other northern areas, owing to the dominant influence on the east coast of Newfoundland of the cold but nutrient rich Labrador Current.

Chapter 5
REFERENCES

Aldridge,D.W. (1982). Reproductive tactics in relation to life cycle bioenergetics in three natural populations of the freshwater snail, *Leptoxis carinata*. *Ecology* 63: 196-208

Bachelet,G. (1980). Growth and recruitment of the tellinid bivalve *Macoma balthica* at the southern limit of its geographical distribution, the Gironde Estuary (S.W. France). *Mar. Biol.* 59: 105-117

Baird,R.H. (1966). Notes on an escallop (*Pecten maximus*) population in Holyhead Harbour. *J. mar. biol. Ass. U.K.* 46: 33-47

Ballinger,R.E. (1977). Reproductive strategies: Food availability as a source of proximal variation in a lizard. *Ecology* 58: 628-635

Barber,B.J., Blake,N.J. (1983). Growth and reproduction of the bay scallop, *Argopecten irradians* (Lamarck) at its southern distributional limit. *J. Exp. mar. biol. ecol.* 66: 247-256

Bayne,B.L. (1971). Oxygen consumption by three species of lamellibranch mollusc in declining ambient oxygen tension. *Comp. Biochem. Physiol.* 40A: 955-970

Bayne,B.L. (1976). Aspects of reproduction in bivalve molluscs. In: *Estuarine Processes* Vol. 1 , Wiley,M. (ed.) Academic Press,New York, pp. 432-448

Bayne,B.L. (1983). Responses to environmental stress: tolerance, resistance and adaptation. Proceedings, 18th European Marine Biology Symposium, Oslo, August 1983, Gray, J.S. (In press)

Bayne,B.L. (1984). Aspects of reproductive behaviour within species of bivalve molluscs. In: *Advances in Invertebrate Reproduction 3*, Engels,W. et al. (eds.) Elsevier, Amsterdam. pp. 357-366

Bayne,B.L., Widdows,J. (1978). The physiological ecology of two populations of *Mytilus edulis L. Oecologia (Berl.)* 37: 137-162

Bayne,B.L., Worrall,C.M. (1980). Growth and production of mussels, *Mytilus edulis* from two populations. *Mar. Ecol. Prog. Ser.* 3: 317-328

Bayne,B.L., Newell,R.C. (1983). Physiological energetics of marine molluscs. In: *The Mollusca. Vol. 4(1)*, Saleuddin, A.S.M., Wilbur,K.M. (eds.) Academic Press, New York. pp. 407-515

Bayne,B.L., Gabbott,P.A., Widdows,J. (1975). Some effects of stress in the adult on the eggs and larvae of *Mytilus edulis. J. mar. biol. Ass. U.K.* 55: 675-689

Bayne,B.L., Widdows,J., Newell,R.I.E. (1976). Physiological measurements on estuarine bivalve molluscs in the field. In: *Biology of Benthic Organisms*, Keeger,B.F., Ceidigh,P.O., Boader,P.J.S. (eds.). Pergamon Press, New York, pp. 57-68

Bayne,B.L., Holland,D.L., Moore,M.N., Lowe,D.M., Widdows,J. (1978). Further studies on the effects of stress in the adult on the eggs of *Mytilus edulis. J. mar. biol. Ass. U.K.* 58: 825-841

Bayne,B.L., Salked,P.N., Worrall,C.M. (1983). Reproductive effort and value in different populations of the marine mussel *Mytilus edulis L. Oecologia* 59: 18-26

Beamish,R.J., Fournier,D.A. (1981). A method for comparing the precision of a set of age determinations. *Can. J. Fish. Aquat. Sci.* 38: 982-983

Beamish,R.J., McFarlane,G.A. (1983). The forgotten requirements for age validation in fisheries biology. *Transactions of the American Fisheries Society.* 112: 735-743

Bell,G. (1980). The costs of reproduction and their consequences. *Am. Nat.* 116: 45-76

Bell,G. (1983). Measuring the cost of reproduction III. The correlation stucture of the early life history of *Dalphnia pulex. Oecologia (Berl.)* 60: 378-383

Bell,G. (1984a). Measuring the cost of reproduction. I. The correlation structure of the life table of a plankton rotifer. *Evolution* 38: 300-313

Bell,G. (1984b). Measuring the cost of reproduction. II. The correlation structure of the life tables of five freshwater invertebrates. *Evolution* 38: 314-326

Bourne,N. (1964). Scallops and the offshore fishery of the Maritimes. *J. Fish. Res. Bd Can.* 145: 1-61

Brannen,R.E. (1940). Growth rate and age group distribution of the giant scallop in the Bay of Fundy. *Fish. Res. Bd Can.,Mans. Rept.* 8 pp.

Briarty,L.G. (1975). Stereology: Methods for quantitative light and electron microscopy. *Science Progress.* 62: 1-32

Brody,M.S., Edgar,M.H., Lawlor,L.R. (1983). A cost of reproduction in a terrestial isopod. *Evolution* 37: 653-655

Broom,M.J. (1983). Mortality and production in natural, artificially seeded and experimental populations of *Anadara granosa* (Bivalvia:Arcidae). *Oecologia (Berl.)* 58: 389-397

Broom,M.J., Mason,J. (1978). Growth and spawning in the pectinid *Chlamys opercularis* in relation to temperature and phytoplankton concentration. *Mar. Biol.* 47: 277-285

Brousseau,D.J. (1979). Analysis of growth rate in *Mya arenaria* using the Von Bertalanffy equation. *Mar. Biol.* 51: 221-227

Browne,R.A,, Russell-Hunter,W.D. (1978). Reproductive effort in molluscs. *Oecologia* 37: 23-27

Caddy,J.F. (1970). A method of surveying scallop populations from a submersible. *J. Fish. Res. Bd Can.* 27: 535-549

Caddy,J.F., Chandler,R.A., Lord,E.I. (1970). Bay of Fundy scallop surveys (1966 and 1967), with observations on the commercial fishery. *Fish. Res. Bd Can. Tech. Report* no. 168. p.1-9

Calow,P. (1979). The cost of reproduction: A physiological approach. *Biol. Rev.* 54: 23-40

Calow,P. (1982). Homeostasis and Fitness. *Am. Nat.* 120: 416-419

Calow,P. (1984). Exploring the adaptive landscapes of invertebrate life cycles. In: *Advances in Invertebrate Reproduction 3*, Engels,W. et al. (eds.) Elsevier, Amsterdam. pp. 329-342

Calow,P., Woollhead,A.S. (1977). The relationship between ration , reproductive effort and age-specific mortality in the evolution of life history strategies: Some observations on freshwater triclads. *J. Anim. Ecol.* 46: 765-781

Ceccherelli,V.U. and Rossi,R. (1984). Settlement, growth and production of the mussel, *Mytilus galloprovincialis*. *Mar. Ecol. Prog. Ser.* 16: 173-184

Chang,W.Y.B. (1982). A statistical method of evaluating the reproducibility of age determinations. *Can. J. Fish. Aquat. Sci.* 39: 1208-1210

Charlesworth,B., Leon,J.A. (1976). The relation of reproductive effort to age. *Am. Nat.* 110: 449-459

Chipman,W.A., Hopkins,J.G. (1954). Water filtration by the bay scallop, *Pecten irradians*, as observed with the use of radioactive plankton. *Biol. Bull. mar. biol. Lab., Woods Hole* 107: 80-91

Crabtree,D.M., Clausen,C.D., Roth,A.A. (1980). Consistency in growth line counts in bivalve specimens. *Palaeogeogr., Paleoclimatol., Palaeoecol.* 29: 323-340

Craig,J.F., Kipling,C. (1983). Reproduction effort versus the environment; Case histories of windermere perch, *Perca fluviatilis* L., and pike, *Esox lucius* L. *J. Fish. Biol.* 22: 713-727

Culling,C.F.A. (1963). Handbook of histopathological techniques 2nd ed. Butterworths, London 533 pp.

D'Amours,D., Pilote,S. (1982). Données biologiques sur le pétoncle d'islande (*Chlamys islandica*) et le pétoncle géant (*Placopecten magellanicus*) de la Basse-Cote-Nord du Québec (secteur de la tabatière). Direction generale des peches maritimes. Cahier d'information no. 99

Dickie,L.M. (1953). Fluctuations in abundance of the giant scallop, *Placopecten magellanicus* (Gmelin), in the Digby area of the Bay of Fundy. *J. Fish. Res. Bd Can., MSS rept. Biol. Sta. No. 526*

Dickie,L.M. (1955). Fluctuations in abundance of the giant scallop, *Placopecten magellanicus* (Gmelin), in the Digby area of the Bay of Fundy. *J. Fish. Res. Bd Can.* 12: 797-857

Dickie,L.M. (1958). Effects of high temperature on survival of the giant scallop. *J. Fish. Res. Bd Can.* 15: 1189-1211

Dickie,L.M., Boudreau,P.R., Freeman,K.R. (1984). Influences of stock and site on growth and mortality in the blue mussel [*Mytilus edulis*]. *Can. J. Fish. Aquat. Sci.* 41: 134- 140

Driscoll,J. (1981). Aquaculture methods in Newfoundland. (An introduction). *Gov't of Newfoundland and Labrador, Dept. of Fisheries. Development Branch Report No. 24* 32 pp.

Elliot,J.M., Davison,W. (1975). Energy equivalents of oxygen consumption in animal energetics. *Oecologia (Berl.)* 19: 195-201

Elner,R.W., Jamieson,G.S. (1979). Predation of the sea scallop, *Placopecten magellanicus*, by the rock crab, *Cancer irroratus* and the American lobster, *Homarus americanus. J. Fish. Res. Bd Can.* 36: 537-543

Fisher,R.A. (1930). The genetical theory of natural selection. Oxford University Press, London

Forgeron,F.D. (1959). Temperature and salinity in the Quoddy region. Chapter 1. In: *Passamaquoddy Fisheries Investegations. Report to the International Joint Commission. Appendix I Oceanography* pp. 1-23

Foster-Smith,R.L. (1975). The effects of concentration of suspension on the filtration rates and pseudofaecal production for *Mytilus edulis* L., *Cerastoderma edule* (L.) and *Venerupis pullastra* (Montagu). *J. exp. mar. Biol. Ecol.* 17: 1-22

Freere,R.H. (1967). Stereologic techniques in microscopy. *Journal of the Royal Microscopical Society* 87: 25-34

Fuji,A., Hashizume,M. (1974). Energy budget for a Japanese common scallop, *Patinopecten yessoensis* (Jay), in Mutsu Bay. *Bull. Fac. Fish. Hokkaido Univ.* 25: 7-19

Gabbott,P.A., Bayne,B.L. (1973). Biochemical effects of temperature and nutritive stress on *Mytilus edulis* L. *J. mar. biol. Ass. U.K.* 53: 269-286

Gadgil,M., Bossert,W.H. (1970). Life historical consequences of natural selection. *Am. Nat.* 104: 1-24

Giese,A.C., Pearse,J.S. (1974). Introduction: General Principles. Chapter 1. In: *Reproduction of Marine Invertebrates*, Giese,A.C., Pearse,J.S. (eds.). Vol. 1. Academic Press, New York, pp. 1-49

Goodman,D. (1979). Regulating reproductive effort in a changing environment. *Am. Nat.* 113: 735-748

Goodman,D. (1982). Optimal life histories, optimal notation and the value of reproductive value. *Am. Nat.* 119: 803-823

Griffiths,C.L., King,J.A. (1979a). Some relationships between size, food availability and energy balance in the ribbed mussel *Aulacomya ater*. *Mar. Biol.* 51: 141-149

Griffiths,C.L., King,J.A. (1979b). Energy expended on growth and gonad output in the ribbed mussel *Aulacomya ater*. *Mar. Biol.* 53: 217-222

Griffiths,R.J. (1981a). Population dynamics and growth of the bivalve *Choromytilus meridionalis* (Kr.) at different tidal levels. *Estuar. coast. Shelf Sci.* 12: 101-118

Griffiths,R.J. (1981b). Production and energy flow in relation to age and shore level in the bivalve *Choromytilus meridionalis* (Kr.). *Estuar. coast. Shelf Sci.* 13: 477-493

Gruffydd,Ll.D. (1972). Mortality of scallops on a Manx seallop bed due to fishing. *J. mar. biol. Ass. U.K.* 52: 449-455

Gruffydd,Ll.D. (1974a). An estimate of natural mortality in an unfished population of the scallop *Pecten maximus* (L.) *J. cons. int. Explor. Mer.* 35: 209-210

Gruffydd,Ll.D. (1974b). The influence of certain environmental factors on the maximum length of the scallop *Pecten maximus* (L.). *J. cons. int. Explor. Mer.* 35: 300-302

Gruffydd,Ll.D. (1981). Observations on the rate of production of external ridges on the shell of *Pecten maximus* in the laboratory. *J. mar. biol. Ass. U.K.* 61: 401-411

Haukioja,E., Hakala,T. (1978). Life-history evolution in *Anodonta piscinalis* (Mollusca, Pelecypoda). *Oecologia (Berl.)* 35: 253-266

Hawkins,A.J.W. (1983). Metabolic strategy in the marine mussel, *Mytilus edulis* L. Unpubl. Ph.D. Thesis, University of Exeter, U.K.(cited in Bayne 1984)

Hickman,R.W. (1979). Allometry and growth of the green- lipped mussel *Perna canaliculus* in New Zealand. *Mar. Biol.* 51: 311-327

Hidu,H., Richmond,M.S., Price,A.H. II (1977). Morphological variability in sea scallops *Placopecten magellanicus* (Gmelin) related to meat yield. *Nat. Shellfish. Assoc.* 67: 75-79

Hirshfield,M.F. (1980). An experimental analysis of reproductive effort and cost in the Japanese Medaka, *Oryzias latipes*. *Ecology* 61: 282-292

Hirshfield,M.F., Tinkle,D.W. (1975). Natural selection and the evolution of reproductive effort. *Proc. Nat. Acad. Sci.* 72: 2227-2231

Hopkins,B., Skellam,J.G. (1954). A new method for determining the type of distribution of plant individuals. *Ann. Bot. Lond. N.S.* 18: 213-227

Hughes,R.N., Roberts,D.J. (1980). Reproductive effort of winkles (*Littorina spp.*) with contrasted methods of reproduction. *Oecologia (Berl.)* 47: 130-136

Hughes,W.W., Clausen,C.D. (1980). Variability in the formation and detection of growth increments in bivalve shells. *Paleobiology* 6: 503-511

Jamieson,G.S., Witherspoon,N.B., Lundy,M.J. (1981a). Assessment of Northumberland Strait scallop stocks-1980. Fisheries and Oceans Canada. *Can. Tech. Rep. of Fish. and Aquat. Sci.* No. 1017. pp. 1-44

Jamieson,G.S., Kerr,G., Lundy,M.J. (1981b). Assessment of scallop stocks on Browns and German Banks-1979. Fisheries and Oceans Canada. *Can. Tech. Rep. of Fish. and Aquat. Sci.* No. 1014. pp. 1-17

Jamieson,G.S., Stone,H., Etter,M. (1982). Predation of sea scallops (*Placopecten magellanicus*) by lobsters (*Homarus americanus*) and rock crabs (*Cancer irroratus*) in underwater cage enclosures. *Can. J. Fish. Aquat. Sci.* 39: 499-505

Johannessen,O.H. (1973). Age determination in *Chlamys islandica* (O.F.Muller). *Astarte* 6: 15-20

Jones,D.S., Thompson,I., Ambrose,W. (1978). Age and growth rate determination for the Atlantic surf clam *Spisula solidissima* (Bivalve: Mactracea) based on internal growth lines in shell cross-sections. *Mar. Biol.* 47: 63-70

Kappenman,R.F. (1981). A method for growth curve comparisons. *Fish. Bull.* 79: 95-101

Kautsky,N. (1982a). Growth and size structure in a Baltic *Mytilus edulis* population. *Mar. Biol.* 68: 117-133

Kautsky,N. (1982b). Quantitative studies on gonad cycle, fecundity, reproductive output and recruitment in a Baltic *Mytilus edulis* population. *Mar. Biol.* 68: 143-160

Kiorboe,T., Mohlenberg,F. (1981). Particle selection in suspension-feeding bivalves. *Mar. Ecol. Prog. Ser.* 5: 291-296

Kirby-Smith,W.W. (1972). Growth of the bay scallop: The influence of experimental water currents. *J. exp. mar. Biol. Ecol.* 8: 7-18

Kirby-Smith,W.W., Barber,R.T. (1974). Suspension-feeding aquaculture systems: Effects of phytoplankton concentration and temperature on growth of the bay scallop. *Aquaculture* 3: 135-145

Knight,W. (1968). Asymptotic growth: An example of nonsense disguised as mathematics. *J. Fish. Res. Bd Can.* 25: 1303- 1307

Kranck,K. (1980). Variability of particulate matter in a small coastal inlet. *Can. J. Fish. Aquat. Sci.* 37: 1209-1215

Kranck,K., Milligan,T. (1979). The use of the coulter counter in studies of particle size-distributions in aquatic environments. *Bedford Institute of Oceanography. Department of Fisheries and Oceans. Report Series BI-R-79-7* pp. 1-48

Kuppusamy,V.N., Ramalingam,K. (1982). An in situ method for measuring the oxygen uptake of wood-boring teredinid molluscs. *Material and Organismen 17 Bd. Heft 2* pp. 117- 126

Larsen,P.F., Lee,R.M. (1978). Observations on the abundance, distribution and growth of postlarval sea scallops, *Placopecten magellanicus*, on Georges Bank. *The Nautilus* 92: 112-116

Leighton,D.L. (1979). A growth profile for the rock scallop *Hinnites multirugosus* held at several depths off La Jolla, California. *Mar. Biol.* 51: 229-232

Lopez-Veiga,E.C., Wells,R., Hodder,V.M. (1977). Report of ageing workshop on cod held at Vigo, Spain, October 1975. *International Comm. for the Northwest Atlantic Fish.* #2 pp. 155-186

Lowe,D.M., Moore,M.N., Bayne,B.L. (1982). Aspects of gametogenesis in the marine mussel, *Mytilus edulis* (L.). *J. mar. biol. Ass. U.K.* 62: 133-145

Lucas,A., Calvo,J., Trancort,M. (1978). L'effort de reproducttion dans la strategie demographique de six bivalves de l'Atlantique. *Haliotis* 9: 107-116

Lutz,R.A. (ed.) (1980). Mussel culture and harvest: A North American perspective. Elsevier, Amsterdam

Lutz,R.A., Rhoads,D.C. (1980). Growth patterns within the molluscan shell. An overview. In: *Skeletal Growth of Aquatic Organisms.* Rhoads,D.C., Lutz,R.A. (eds.) Plenum Press, New York. pp. 203-254

MacKenzie,C.L. Jr. (1979). Biological and fisheries data on sea scallop *Placopecten magellanicus* (Gmelin). *U.S. Dept. of Commerce Tech. Rep. No. 19*

Mäntylä,K. (1981). Pikkujärvisimpukan (*Anodonta piscinalis,*) (Nilsson) jälkeläistuotto ja lisääntymispanos *M. Sc. thesis, University of Turku* (cited in Tuomi et al., 1983)

Mason,J. (1957). The age and growth of the scallop *Pecten maximus* in Manx waters. *J. mar. biol. Ass. U.K.* 36: 473-492

Menge,B.A. (1974). Effect of wave action and competition on brooding and reproductive effort in the seastar, *Leptasterias hexactis. Ecology* 55: 84-93

Merrill,A.S., Posgay,J.A. (1964). Estimating the natural mortality rate of the sea scallop (*Placopecten magellanicus*). *ICNAF Research Bulletin No. 1* pp. 88-98

Merrill,A.S., Posgay,J.A., Nichy,F.E. (1966). Annual marks on shell and ligament of sea scallop *Placopecten magellanicus*. *Fish. Bull.* 65: 299-311

Misra,R.K. (1980). Statistical comparisons of several growth curves of the Von Bertalanffy type. *Can. J. Fish. Aquat. Sci.* 37: 920-926

Mohlenberg,F., Kiorboe,T. (1981). Growth and energetics in *Spisula subtruncata* (Da Costa) and the effect of suspended bottom material. *Ophelia* 20: 79-90

Naidu,K.S. (1969). Growth, reproduction and unicellular endosymbiotic alga in the giant scallop *Placopecten magellanicus* (Gmelin) in Port au Port Bay, Newfoundland. *M. Sc. thesis, Memorial University of Newfoundland* 181 p.

Naidu,K.S. (1970). Reproduction and breeding cycle of the giant scallop *Placopecten magellanicus* (Gmelin) in Port au Port Bay, Newfoundland. *Can. J. Zool.* 48: 1003- 1012

Neter,J., Wasserman,W., Kutner,M.H. (1983). *Applied linear regression models.* Irwin Publishers Homeland, Illinois pp.547

Newell,R.C. (1979). Biology of intertidal animals. *Marine Ecological Surveys, Faversham*

Newell,R.I.E. (1982). An evaluation of the wet oxidation technique for use in determining the energy content of seston samples. *Can. J. Fish. Aquat. Sci.* 39: 1383- 1388

Newell,R.I.E., Bayne,B.L. (1980). Seasonal changes in the physiology, reproductive

condition and carbohydrate content of the cockle *Cardium* (=*Cerastoderma* edule) (Bivalvia: Cardiidae]. *Mar. Biol.* 56: 11-19

Newell,R.I.E., Jordan,S.J. (1983). Preferential ingestion of organic material by the American oyster *Cassostrea virginica*. *Mar. Ecol. Prog. Ser.* 13: 47-53

Newell,R.I.E., Hilbish,T.J., Koehn,R.K., Newell,C.J. (1982). Temporal variation in the reproductive cycle of *Mytilus edulis* (L.) (Bivalvia: Mytilidae) from localities on the east coast of the United States. *Biol. Bull.* 162: 299-310

Nichols,D., Barker,M.F. (1984). A comparative study of reproductive and nutritional periodicities in two populations of *Asterias rubens* (Echinodermata: asteriodea) from the English Channel. *J. mar. biol. Ass. U.K.* 64: 471-484

Nichols,J.D., Conley,W., Batt,B., Tipton,A.R. (1976). Temporally dynamic reproductive strategies and the concept of r- and K- selection. *Am. Nat.* 110: 995-1005

Ockelmann,K.W. (1958). The zoology of East Greenland marine Lamellibranchiata. *Medd. Groenl.* 122: 1-256

Paine,R.T. (1976). Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction *Ecology* 57: 858-873

Parry,G.D. (1982). Reproductive effort in four species of intertidal limpets. *Mar. Biol.* 67: 267-282

Pfitzenmeyer,H.T. (1965). Annual cycle of gametogenesis of the soft-shell clam, *Mya arenaria* at Solomon, Maryland. *Ches. Sci.* 6: 52-59

Posgay,J.A. (1957). The range of the sea scallop. *The Nautilus* 71: 55-57

Posgay,J.A. (1979). Depth as a factor affecting the growth rate of the sea scallop. *I.C.E.S. Document CM 1979/K:27*

Rafail,S.Z. (1972). Fitting a parabola to growth data of fishes and some application to fisheries. *Mar. Biol.* 15: 255-264

Richardson,C.A., Taylor,A.C., Venn,T.J. (1982). Growth of the queen scallop *Chlamys opercularis* in suspended cages in the Firth of Clyde. *J. mar. biol. Ass. U.K.* 62: 157-169

Robinson,W.E., Wehling,W.E., Morse,M.P., McLeod,G.C. (1981). Seasonal changes in soft-body component indices and energy reserves in the Atlantic deep-sea scallop, *Placopecten magellanicus*. *Fish. Bull.* 79: 449-458

Robinson,W.E., Wehling,W.E., Morse,M.P. (1984). The effect of suspended clay on feeding and digestive efficiency of the surf clam, *Spisula solidissima* (Dillwyn). *J. exp. mar. Biol. Ecol.* 74: 1-12

Rodhouse,P.G. (1979). A note on the energy budget for an oyster population in a temperate estuary. *J. exp. mar. Biol. Ecol.* 37: 205-212

Rodhouse,P.G., Roden,C.M., Hensey,M.P., McMahon,T., Ottway,B., Ryan,T.H. (1984). Food resource, gametogenesis and growth of *Mytilus edulis* on the shore and in suspended culture: Killary Harbour, Ireland. *J. mar. biol. Ass. U.K.* 64: 513-529

Roff,D.A. (1980). A motion for the retirement of the Von Bertalanffy function. *Can. J. Fish. Aquat. Sci.* 37: 127-129

Sastry,A.N. (1966). Temperature effects in reproduction of the bay scallops, *Aequipecten irradians* Lamarck. *Biol. Bull.* 130: 118-134

Sastry,A.N. (1970). Reproductive physiological variation in latitudinally separated

populations of the bay scallop, *Aequipecten irradians* Lamarck. *Biol. Bull.* 138: 56-65

Sastry,A.N. (1979). Pelecypoda (excluding Ostreidae). In: *Reproduction of Marine Invertebrates. Vol. V* Giese,A.C., Pearse,J.S. (eds.) Academic Press, New York. pp. 113-292

Sastry,A.N., Blake,N.J. (1971). Regulation of gonad development in the bay scallop, *Aequipecten irradians* Lamarck. *Biol. Bull.* 140: 274-283

Sebens,K.P. (1979). The energetics of asexual reproduction and colony formation in benthic marine invertebrates. *Am. Zool.* 19: 683-697

Sebens,K.P. (1982). The limits to indeterminate growth: An optimal size model applied to passive suspension feeders. *Ecology* 63: 209-222

Seed,R. (1976). Ecology. In: *Marine mussels - their ecology and physiology* Bayne,B.L. (ed.) Cambridge University Press, Cambridge. pp. 13-65

Seed,R. (1980). Shell growth and form in the bivalvia. In: *Skeletal growth of aquatic organisms*, Rhoads,D.C., Lutz, R.A. (eds.) Plenum Press, New York. pp. 23-68

Seed,R., Brown,R.A. (1978). Growth as a strategy for survival in two marine bivalves, *Cerastoderma edule* and *Modiolus modiolus*. *J. Anim. Ecol.* 47: 283-292

Shafee,M.S., Lucas,A. (1980). Quantitative studies on the reproduction of the black scallop *Chlamys varia* (L.) from Lanevoc area (Bay of Brest). *J. exp. mar. Biol. Ecol.* 42: 171-186

Shafee,M.S., Lucas,A. (1982). Variations saisonnieres du bilan energetique chez les individus d'une population de *Chlamys varia* (L.): Bivalvia, Pectinidae. *Oceanologica Acta* 5: 331-338

Sheldon,R.W., Prakash,A., Sutcliffe,W.H.,Jr. (1972). The distribution of particles in the ocean. *Limnol. Oceanogr.* 17: 327-340

Skreslet,S., Brun,E. (1969). On the reproduction of *Chlamys islandica* (O.F. Muller) and its relation to depth and temperature. *Astarte* 2: 1-6

Snedecor,G.W., Cochran,W.G. (1972). Statistical methods. The Iowa State University Press, Iowa. pp. 593

Sokal,R.R., Rohlf,F.J. (1981). *Biometry* 2nd ed., W.H. Freeman and Co., San Francisco. 859 pp.

Sprung,M. (1983). Reproduction and fecundity of the mussel *Mytilus edulis* at Helgoland (North Sea). *Helgolander Meeresunters* 36: 243-255

Spight,T.M., Emlen,J. (1976). Clutch sizes of two marine snails with a changing food supply. *Ecology* 57: 1162-1178

Stearns,S.C. (1976). Life-history tactics: A review of the ideas. *The Quarterly Review of Biology* 51: 3-47

Stearns,S.C. (1980). A new view of life-history evolution. *Oikos* 35: 266-281

Stearns,S.C. (1983). On fitness. In: *Fourth Bromen Symp. Biol. Systems Theory* (cited in Tuomi et al., 1983)

Stearns,S.C. (1984). The tension between adaption and constraint in the evolution of reproductive patterns. In: *Advances in Invertebrate Reproduction 3* Engels,W. et al. (eds.) Elsevier, Amsterdam. pp. 387-398

Stevenson,J.A., Dickie,L.M. (1954). Annual growth rings and rate of growth of the giant scallop, *Placopecten magellanicus* (Gmelin) in the Digby area of the Bay of Fundy. *J. Fish. Res. Bd Can.* 11: 660-671

Strickland,J.D.H., Parsons,T.R. (1972). A practical handbook of seawater analysis. *Fish. Res. Bd Can. Bull. 167*

Sundet,J.H., Lee,J.B. (1984). Seasonal variations in gamete development in the Iceland scallop, *Chlamys islandica*. *J. mar. biol. Ass. U.K.* 64: 411-416

Taylor,J.D., Kennedy,W.J., Hall,A. (1969). The shell structure and mineralogy of the bivalvia. Introduction. Nuculacea- Trigonacea. *Bull. Br. Mus. nat. Hist. (Suppl.)* 3: 1-125

Thompson,R.J. (1977). Blood chemistry, biochemical composition and the annual reproductive cycle in the giant scallop, *Placopecten magellanicus*, from southeast Newfoundland. *J. Fish. Res. Bd Can.* 34: 2104-2116

Thompson,R.J. (1979). Fecundity and reproductive effort in the blue mussel (*Mytilus edulis*), the sea urchin (*Strongylocentrotus droebachiensis*) and the snow crab (*Chinoecetes opilio*) from populations in Nova Scotia and Newfoundland. *J. Fish. Res. Bd Can.* 36: 955- 964

Thompson,R.J. (1983). The relationship between food ration and reproductive effort in the green sea urchin, *Strongylocentrotus droebachiensis*. *Oecologia* (Berlin) 56: 50-57

Thompson,R.J. (1984a). Production, reproductive effort, reproductive value and reproductive cost in a population of the blue mussel *Mytilus edulis* from a subarctic environment. *Mar. Ecol. Prog. Ser.* 16: 249-257

Thompson,R.J. (1984b). The reproductive cycle and physiological ecology of the mussel *Mytilus edulis* in a subarctic, non-estuarine environment. *Mar. Biol.* 79: 277-288

Tuomi,J., Hakala,T., Haukioja,E. (1983). Alternative concepts of reproductive effort, costs of reproduction and selection in life-history evolution. *Am. Zool.* 23: 25-34

Ursin,E. (1963). On the incorporation of temperature in the Von Bertalanffy growth equation. *Meddr. Danm. Fisk.-og. Havunders* 4: 1-16

Vahl,O. (1978). Seasonal changes in oxygen consumption of the Iceland scallop *Chlamys islandica* (O.F. Muller) from 70 ° N. *Ophelia* 17: 143-154

Vahl,O. (1980). Seasonal variations in seston and the growth rate of the Iceland scallop, *Chlamys islandica* (O.F. Muller) from Balsfjord, 70 ° N. *J. exp. mar. Biol. Ecol.* 48: 195-204

Vahl,O. (1981a). Age-specific residual reproductive value and reproductive effort in the Iceland scallop, *Chlamys islandica* (O.F. Muller). *Oecologia* 51: 53-56

Vahl,O. (1981b). Energy transformations by the Iceland scallop, *Chlamys islandica* (O.F. Muller), from 70 ° N. 1. The age-specific energy budget and net growth efficiency. *J. exp. mar. Biol. Ecol.* 53: 281-296

Vahl,O. (1982). Long-term variations in recruitment of the Iceland scallop, *Chlamys islandica* from Northern Norway. *Neth. J. Sea Res.* 16: 80-87

Velez,A., Epifanio,C.E. (1981). Effects of temperature and ration on gametogenesis and growth in the tropical mussel *Perna perna* (L.). *Aquaculture* 22: 21-26

Ventilla,R.F. (1982). The scallop industry in Japan. *Adv. Mar. Biol.* 20: 309-382

Warwick,R.M. (1980). Population dynamics and secondary production of benthos. In: *Marine Benthic Dynamics*, Tenore,K.R., Coull,B.C. (eds.) Univ. S. Carolina Press. pp. 451

Weibel,E.R., Elias,H. (1967). Quantitative methods in morphology. Springer-Verlag. pp. 267

Widdows,J., Bayne,B.L. (1971). Temperature acclimation of *Mytilus edulis* with reference to its energy budget. *J. mar. biol. Ass. U.K.* 51: 827-843

Widdows,J. (1978). Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. *J. mar. biol. Ass. U.K.* 58: 109-124

Widdows,J., Fieth,P., Worrall,C.M. (1979). Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis*. *Mar. Biol.* 50: 195- 207

Williams,G.C. (1966). Natural selection, the cost of reproduction and a refinement of Lack's principle. *Am. Nat.* 100: 687-690

Wilton,G. (1981). Exploratory fishing for scallops in selected areas from Bonne Bay to Strait of Belle Isle 1980. Government of Newfoundland and Labrador, Dept. Fisheries Development Branch Report No. 20 37 p.

Woollhead,A.S., Calow,P. (1979). Energy-partitioning strategies during egg production in semelparous and iteroparous triclads. *J. Animal Ecol.* 48: 491-499

Worrall,C.M., Widdows,J., Lowe,D.M. (1983). Physiological ecology of three populations of the bivalve *Scrobicularia plana*. *Mar. Ecol. Prog. Ser.* 12: 267-279

Zar,J.H. (1984). Biostatistical analysis. 2nd ed. Prentice Hall, New Jersey. pp. 718

Chapter 6
APPENDIX

Appendix A

A.1. Regression equations and comparisons.

Table A-1: Parameters and statistics for regressions of clearance and metabolic rates against dry tissue weight, after logarithmic transformation of both variates. F values are significant to at least $P<.001$ unless otherwise noted where $*=P<.05$ and $**=P<.01$.

CLEARANCE

10m	log a	b	n	r^2	F
July	-0.21	0.76	22	0.88	141
September	0.12	0.60	19	0.88	126
November	-0.05	0.66	20	0.91	188
31m					
July	-0.05	0.68	17	0.91	157
September	-0.06	0.70	20	0.85	100
November	-0.14	0.68	21	0.81	83

O_2 Consumption

10m					
July	-0.35	0.70	22	0.89	168
September	-0.47	0.78	19	0.92	191
November	-0.88	0.88	20	0.94	289
31m					
July	-0.67	0.76	17	0.90	132
September	-0.63	0.79	20	0.80	73
November	-1.18	0.93	21	0.96	464

Table A-2: Parameters and statistics for shell height versus age fitted to polynomial equations. Abbreviations for sites are in Figure 2-1.

Site	Dep(m)	β_0	β_1	β_2	β_3	n	r^2	F
SS								
	10m	146.8	5.7	-0.64	0.03	272	0.97	2929
	20m	141.7	5.3	-0.63	0.03	256	0.97	3050
	31m	127.3	5.1	-0.48	0.02	243	0.97	2673
DB								
	10m	145.3	5.2	-0.63	0.05	121	0.97	1305
	20m	140.9	5.2	-0.57	0.03	148	0.96	1244
	31m	129.7	3.8	-0.58	0.05	137	0.97	1442
TN								
	10m	143.2	4.9	-0.68	0.04	114	0.90	326
	20m	133.6	3.6	-0.52	0.04	122	0.94	618
	31m	122.1	3.6	-0.37	0.03	94	0.92	358
St. A								
	10m	108.6	13.3	-1.33	0.02	83	0.96	660
	31m	105.9	13.6	-1.20	-0.02	73	0.98	1094
	76m	106.5	12.5	-1.20	0.01	58	0.97	600
Cl								
	6m	130.8	4.7	-0.55	0.04	280	0.96	2400
	16m	132.7	5.4	-0.58	0.03	207	0.96	1765
SC	10m	102.9	8.3	-2.38	0.50	200	0.89	514
NJ	31m	97.5	15.5	-1.28	-0.24	137	0.95	918
SH	10m	91.6	13.8	-1.27	0.05	84	0.98	1226

Table A-3: Summary of t values for comparisons of shell height versus age fitted to polynomial equations.

	Sunnyside	Dildo	TNNP	St. Andrews	Colinet
Dep (m)					
10m+20m				(10m+76m)	(6m+16m)
β_0	6.61***	4.46***	8.94***	1.52	2.57*
β_1	1.51	0.22	3.37***	0.92	2.31*
β_2	0.14	1.48	2.37	0.67	0.86
β_3	0.68	2.28	0.05	0.14	1.73
20m+31m				(31m+76m)	
β_0	16.51***	11.87***	11.05***	0.34	
β_1	0.74	4.60***	0.11	1.23	
β_2	5.3***	0.20	3.14**	0.02	
β_3	0.98	2.15	1.37	0.30	
10m+31m					
β_0	22.57***	15.26***	19.05***	1.99	
β_1	2.28	4.14	3.20**	0.35	
β_2	5.44***	1.25	4.81***	0.67	
β_3	1.68	0.21	1.39	0.60	

Table A-4: Summary of comparisons of the Von Bertalanffy parameters, NS = nonsignificant $P<0.05$

	Sunnyside	Dildo	TNNP	St. Andrews	Colinet
Dep(m)					
10m+20m				(10m+76m)	(6m+16m)
H_∞	*	*	*	NS	NS
k	NS	NS	NS	NS	NS
t_0	NS	NS	*	NS	NS
20m+31m				(31m+76m)	
H_∞	*	*	NS	NS	
k	*	NS	*	NS	
t_0	*	NS	*	NS	
10m+31m					
H_∞	*	*	*	NS	
k	*	NS	*	NS	
t_0	*	NS	*	NS	

Table A-5: Summary of t values for comparisons of shell weight versus shell height.

Dep (m)	Sunnyside	Dildo	TNNP	St. Andrews	Colinet
10m+20m				(10m+76m)	(6m+16m)
a	4.10***	3.08**		0.48	-
b	4.42***	0.73	3.17**	2.31	4.35***
20m+31m				(31m+76m)	
a	4.42***	-	10.15***	-	
b	0.03	2.72**	0.68	5.00***	
10m+31m					
a	8.63***	7.91***	11.36***	-	
b	1.01	1.91	2.29	2.95**	

Table A-6: Summary of t values for comparisons of somatic weight versus age fitted to polynomial equations.

Dep (m)	Sunnyside	Dildo	TNNP	St. Andrews	Colinet
10m+20m				(10m+76m)	(6m+16m)
β_0	8.29***	12.75***	12.00***	0.14	8.48***
β_1	3.16**	9.56***	7.92***	1.96	5.06***
β_2	0.68	3.32**	2.34	2.41	4.63***
β_3	0.34	-	-	-	-
20m+31m				(31m+76m)	
β_0	12.69***	12.87***	10.77***	1.15	
β_1	5.33***	8.96***	3.45**	1.89	
β_2	2.32	2.07	2.64**	1.57	
β_3	0.90	-	-	-	
10m+31m					
β_0	20.06***	24.64***	22.36***	1.17	
β_1	8.77***	17.86***	10.36***	0.03	
β_2	2.96**	5.08	4.66***	1.05	
β_3	0.59	-	-	-	

Table A-7: Summary of t values for comparisons of somatic weight versus shell height.

Dep(m)	Sunnyside	Dildo	TNNP	Colinet
1981				
10m+20m				
a	5.48***	5.33***		-
b	1.10	0.88		2.39*
20m+31m				
a	9.16***	4.76***		
b	1.46	0.96		
10m+31m				
a	14.27***	9.29***		
b	0.38	1.60		
1982				
10m+20m				(6m+16m)
a	1.81	4.33***	3.99***	3.45***
b	0.58	0.61	0.45	1.90
20m+31m				
a	-	5.07***	2.82**	
b	2.66**	0.07	1.58	
10m+31m				
a	-	9.33***	5.99***	
b	3.08**	0.72	0.90	

Table A-8: Summary of t values for comparisons of somatic weight versus shell height.

Dep.(m)	Sunnyside	Dildo	TNNP	St. Andrews	Colinet
1983					
10m+20m				(10m+76m)	(6m+16m)
a	2.41**	1.14	5.16***	5.27***	0.69
b	1.03	0.41	0.27	1.43	0.90
20m+31m				(31m+76m)	
a	4.58***	7.14***	0.86	3.24**	
b	2.28	0.65	0.08	0.28	
10m+31m					
a	-	9.03***	6.26***	2.04	
b	4.53***	0.24	0.16	1.78	

Table A-9: Summary of t values for comparisons of shell height versus age fitted to polynomial equations

Dep (m)	Sunnyside+Dildo	Dildo+TNNP	Sunnyside+TNNP
10m			
β_0	1.37	1.73	3.48***
β_1	1.63	0.65	2.44*
β_2	0.11	0.65	0.67
β_3	1.83	0.49	0.98
20m			
β_0	0.89	7.60***	9.44***
β_1	0.31	4.51***	5.12***
β_2	1.95	1.11	2.86**
β_3	0.18	1.27	1.51
31m			
β_0	2.67**	7.77***	5.62***
β_1	4.66***	0.48	4.55***
β_2	2.83**	5.07***	3.11**
β_3	3.38***	2.20	0.56

Table A-10: Summary of comparisons of the Von Bertalanffy parameters, NS = nonsignificant $P<0.05$

Dep(m)	Sunnyside+Dildo	Dildo+TNNP	Sunnyside+TNNP
10m			
$H\infty$	NS	*	*
k	NS	*	*
t_0	NS	NS	*
20m			
$H\infty$	NS	*	*
k	NS	*	NS
t_0	NS	NS	NS
31m			*
$H\infty$	*	NS	*
k	*	*	NS
t_0	NS	*	*

Table A-11: Summary of t values for comparisons of somatic weight versus age fitted to polynomial equations.

Dep(m)	Sunnyside+Dildo	Dildo+TNNP	Sunnyside+TNNP
10m			
β_0	7.00***	13.56***	8.84***
β_1	7.07***	7.86***	3.61***
β_2	2.45*	2.10	0.28
20m			
β_0	1.40	13.09***	13.21***
β_1	3.47***	10.42***	8.77***
β_2	0.64	1.78	2.54*
31m			
β_0	0.75	9.85***	9.73***
β_1	0.17	6.38***	6.94***
β_2	0.02	2.44*	2.70**

Table A-12: Summary of t values for comparisons of somatic weight versus shell height.

Dep(m)	Sunnyside+Dildo			Dildo+TNNP		Sunnyside+TNNP	
10m							
	1981	1982	1983	1982	1983	1982	1983
a	-	5.6***	6.2***	6.5***	-	-	-
b	2.0*	0.7	0.3	1.9	2.4*	2.8**	2.4*
20m							
a	2.9**	2.6*	2.1*	-	8.1***	-	6.6***
b	1.0	0.9	1.4	2.1*	1.6	3.8***	0.9
31m							
a	2.2*	2.0*	-	4.3***	4.3***	2.7**	1.3
b	0.3	1.1	3.5***	0.4	1.0	0.6	0.3

Table A-13: Summary of t values for yearly comparisons of cubic polynomials fitted to shell height versus age for scallops from Sunnyside and Colinet.

AGE 2-19 YEARS

Years	6m	10m	16m	20m	31m
81+82					
β_0	1.00	1.23	1.01	3.07**	1.43
β_1	0.14	1.48	0.34	0.08	0.45
β_2	1.90	0.44	0.79	3.54	0.06
β_3	0.97	0.15	0.38	1.04	0.49
82+83					
β_0	2.75**	2.28	1.46	0.37	1.35
β_1	0.06	2.27	1.74	0.70	1.16
β_2	0.96	0.05	0.07	0.51	1.52
β_3	0.02	2.52*	1.02	1.53	0.60
81+83					
β_0	2.14	1.29	2.52*	2.01	0.11
β_1	2.69**	3.93***	1.44	0.76	2.09
β_2	0.85	2.97**	0.72	2.09	2.41*
β_3	0.05	0.41	0.57	0.90	0.14

Table A-14: Summary of t values for yearly comparisons of cubic polynomials fitted to shell height versus age for scallops from Sunnyside and Colinet.

AGE 5-19 YEARS

Years	6m	10m	16m	20m	31m
81+82					
β_0	0.18	0.38	0.81	2.33	1.91
β_1	0.78	0.92	0.25	1.04	0.52
β_2	1.67	1.06	0.10	1.91	1.28
β_3	0.34	0.89	0.62	0.03	0.66
82+83					
β_0	1.83	1.28	1.13	0.34	1.70
β_1	0.69	2.54*	1.51	0.47	0.69
β_2	0.07	1.51	0.39	1.14	1.75
β_3	0.52	2.75**	0.30	0.38	0.32
81+83					
β_0	1.80	1.05	1.93	2.31	0.18
β_1	0.02	3.59***	1.32	0.23	1.48
β_2	1.36	0.62	0.44	2.69**	0.42
β_3	0.02	2.26	0.32	0.62	0.38

Table A-15: Summary of t values for comparisons of quadratic polynomials fitted to somatic weight versus age for scallops from Sunnyside and Colinet.

AGE 2-19 YEARS

Years		6m	10m	16m	20m	31m
81+82						
	β_0	1.39	0.98	2.55*	0.66	2.52*
	β_1	0.27	1.92	2.73**	1.31	0.28
	β_2	1.55	0.70	1.82	0.53	1.88
	β_3	-	1.83	-	1.69	0.10
82+83						
	β_0	0.56	2.30	1.83	1.99	2.68**
	β_1	0.43	0.52	0.75	1.39	0.25
	β_2	0.29	1.23	0.72	1.20	2.82**
	β_3	-	0.31	-	1.97	0.33
81+83						
	β_0	1.69	1.56	4.30***	1.36	0.28
	β_1	0.73	1.29	2.14	0.57	0.69
	β_2	1.63	0.62	2.39	0.81	1.51
	β_3	-	1.50	-	0.94	0.61

Table A-16: Summary of t values for comparisons of quadratic polynomials fitted to somatic weight versus age for scallops from Sunnyside and Colinet.

AGE 5-19 YEARS

	6m	10m	16m	20m	31m
81+82					
β_0			2.56*		2.42
β_1			2.16		0.05
β_2			1.66		1.39
β_3			-		0.36
82+83					
β_0			1.36		2.18
β_1			0.86		0.08
β_2			0.08		1.76
β_3			-		0.28
81+83					
β_0			3.74***		0.18
β_1			1.60		0.04
β_2			1.63		0.30
β_3			-		0.08

Table A-17: Summary of t values for yearly comparisons of somatic weight versus shell height.

81+82	6m		10m		16m		20m		31m	
	a	b	a	b	a	b	a	b	a	b
SS			-	4.4***			-	3.2*	0.5	- 0.3
DB			0.1	0.3			3.7***	0.1	3.6***	1.0
Cl	2.7**	1.3			3.7***	0.1				
SC			-	3.6***						
82+83										
SS			1.4	0.8			0.9	1.9	1.5	2.2
DB			1.3	0.3			1.3	0.6	2.4	1.4
Cl	3.3**	2.3			2.0	0.4				
SC			5.1***	2.3						
TN			2.5*	0.7			3.3**	0.1	2.2	1.0
NJ									0.2	0.6
81+83	6m		10m		16m		20m		31m	
SS			-	3.7***			2.9**	0.2	-	2.4*
DB			1.1	0.1			2.5*	0.7	6.1***	2.2
Cl	-	3.8***			5.6***	0.4				
SC			3.1**	1.7						

Table A-18: Parameters and statistics for somatic weight versus shell height regressions.

	1981			1982			1983		
	10m	20m	31m	10m	20m	31m	10m	20m	31m
SS									
log a	-4.15	-4.32	-4.23	-4.81	-4.73	-4.31	-4.67	-4.38	-3.76
b	2.54	2.60	2.52	2.83	2.79	2.55	2.77	2.62	2.28
n	121	134	122	82	90	75	93	56	97
r^2	0.97	0.98	0.96	0.97	0.97	0.94	0.97	0.96	0.83
F	3745	6231	3290	2909	2603	1144	3391	1308	476
DB									
log a	-4.69	-4.52	-4.32	-4.59	-4.49	-4.54	-4.65	-4.65	-4.82
b	2.81	2.68	2.55	2.76	2.69	2.68	2.80	2.76	2.83
n	31	44	48	51	72	49	56	61	62
r^2	0.95	0.97	0.92	0.95	0.93	0.96	0.95	0.96	0.96
F	522	1209	513	950	989	1242	990	1516	1598
Cl	6m	16m		6m	16m		6m	16m	
log a	-4.65	-4.01		-4.50	-4.04		-4.13	-3.96	
b	2.73	2.45		2.64	2.44		2.47	2.39	
n	137	110		85	77		68	69	
r^2	0.97	0.81		0.97	0.90		0.98	0.92	
F	4346	462		2345	666		3298	746	

Table A-19: Parameters and statistics for somatic weight versus shell height regressions.

Site	Yr	Dep(m)	log a	b	n	r^2	F
TN	82	10m	-4.12	2.49	71	0.89	543
		20m	-4.04	2.43	76	0.93	920
		31m	-4.49	2.63	49	0.93	621
	83	10m	-3.87	2.36	34	0.92	372
		20m	-4.08	2.42	29	0.82	126
		31m	-4.04	2.40	34	0.87	217
SC	81	10m	-5.31	3.12	88	0.96	1972
	82	10m	-4.35	2.69	72	0.93	917
	83	10m	-4.97	2.97	40	0.98	1783
SH	83	10m	-4.10	2.50	84	0.97	2683
NJ	82	31m	-4.78	2.78	90	0.95	1808
	83	31m	-4.94	2.86	48	0.93	660
ST.A	83	10m	-4.77	2.83	83	0.99	6493
		31m	-4.55	2.72	75	0.99	5055
		76m	-4.58	2.75	58	0.99	4666

Table A-20: Summary of t values for comparisons of somatic weight versus shell height regressions for males and females.

Sites	6m	10m	16m	20m	31m
Sunnyside					
a		1.44		0.65	-
b		0.78		0.57	4.28***
Dildo					
a		0.32		1.58	0.83
b		0.34		0.73	0.92
TNNP					
a		0.88		1.09	0.79
b		0.41		1.51	1.47
Colinet					
a	0.15		0.11		
b	0.00		0.73		

Table A-21: Summary of t values for the comparisons of prespawned gonad weight versus shell height regressions for males and females.

1981	6m		10m		16m		20m		31m	
	a	b	a	b	a	b	a	b	a	b
SS			0.0	1.0			2.2*	1.3	1.2	0.4
DB			1.9	1.9			1.6	1.2	1.3	0.7
Cl	1.0	1.5			-	2.4*				
1982										
SS			0.5	0.0			1.7	1.1	-	2.2*
DB			1.3	0.8			1.1	0.3	1.7	1.3
Cl	0.7	0.6			-	3.3**				
TN			0.8	0.0			1.3	1.2	1.7	0.4
1983										
SS			-	3.2**			3.2**	1.5	-	2.9**
DB			0.1	0.0			0.1	1.2	-	3.3**
Cl	0.2	1.0			0.7	1.3				
TN			2.3*	0.9			0.2	0.9	0.7	0.6

Table A-22: Summary of t values for comparisons of prespawned gonad weight versus shell height regressions.

Years	6m		10m		16m		20m		31	
81+82	a	b	a	b	a	b	a	b	a	b
SS			-	3.2**			2.5*	0.7	0.9	1.0
DB			7.2***	1.7			12.8***	1.8	7.9***	1.4
Cl	0.4	0.6			0.4	0.9				
SC			2.5*	2.2						
82+83										
SS			2.4*	1.7			0.9	2.3	1.2	0.5
DB			6.7***	0.8			-	3.9***	2.9*	0.4
Cl	3.2**	0.8			0.8	1.7				
SC			2.7*	2.0						
TN			1.3	1.6			0.9	0.8	-	5.8***
NJ									-	2.0*
81+83										
SS			2.1	1.0			1.5	1.6	0.6	0.8
DB			3.5***	1.0			8.5***	0.1	-	2.5*
Cl	4.3***	0.3			0.9	1.7				
SC			1.8	0.4						

Table A-23: Summary of t values for comparison of postspawned gonad weight versus shell height regressions.

Years	6m		10m		16m		20m		31m	
81+82	a	b	a	b	a	b	a	b	a	b
SS			0.3	2.1			1.1	0.7	1.5	0.6
DB			1.2	0.1			1.5	0.2	-	2.7**
Cl	-	3.4***			0.0	0.5				
SC			-	3.0**						
82+83										
SS			1.4	1.1			3.5***	0.2	1.9	1.1
DB			-	3.3***			0.5	1.8	1.8	0.0
Cl	1.9	1.3			0.3	1.0				
SC			-	3.9***						
NJ									4.6***	1.1
81+83										
SS			0.8	0.9			2.8**	0.7	1.0	1.9
DB			1.9	1.9			1.04	1.91	-	2.6*
Cl	4.3***	1.6			0.6	0.3				
SC			0.2	1.3						

Table A-24: Parameters and statistics for prespawned gonad weight versus shell height regressions.

	1981			1982			1983		
	10m	20m	31m	10m	20m	31m	10m	20m	31m
SS									
log a	-5.55	-6.93	-4.41	-7.59	-7.41	-6.16	-6.29	-5.08	-5.75
b	2.90	3.56	2.26	3.97	3.86	3.11	3.29	2.72	2.87
n	44	42	39	37	41	36	41	32	48
r^2	0.73	0.77	0.23	0.87	0.80	0.79	0.83	0.74	0.60
F	116	134	10.8**	235	155	128	187	83	69
DB									
log a	-6.11	-3.65	-6.37	-3.70	-7.06	-7.58	-4.90	-3.60	-7.91
b	3.09	1.87	3.10	2.17	3.68	3.85	2.60	1.99	4.07
n	19	22	24	11	43	17	29	32	31
r^2	0.75	0.23	0.87	0.78	0.79	0.76	0.78	0.60	0.89
F	52	5.8*	151	32	154	48	98	45	240

	6m	16m	6m	16m	6m	16m
Cl						
log a	-7.13	-2.99	-7.60	-4.78	-6.69	-7.29
b	3.44	1.57	3.68	2.40	3.34	3.55
n	45	44	33	27	36	37
r^2	0.82	0.17	0.74	0.27	0.81	0.74
F	203	8.6**	87	9.2**	145	101

Table A-25: Parameters and statistics for prespawned gonad weight versus shell height regressions.

SITE	YR	DEP	log a	b	n	r^2	F
TN	82	10m	-2.08	1.29	48	0.13	7.1*
		20m	-6.00	3.05	54	0.69	115
		31m	-9.31	4.67	34	0.90	285
	83	10m	-5.16	2.70	31	0.29	12**
		20m	-4.74	2.47	29	0.39	17.0
		31m	-2.48	1.35	34	0.26	11.1**
SC	81	10m	-9.65	4.95	44	0.79	159
	82	10m	-7.00	3.73	33	0.87	201
	83	10m	-9.19	4.79	20	0.96	448
SH	83	10m	-6.86	3.58	41	0.77	132
NJ	82	31m	-10.43	5.35	62	0.86	369
	83	31m	-7.89	4.18	24	0.95	402
ST.A	83	10m	-9.96	5.05	43	0.92	477
		31m	-8.21	4.16	41	0.93	513
		76m	-9.58	4.93	18	0.98	668

Table A-26: Parameters and statistics for postspawned gonad weight versus shell height regressions.

	1981			1982			1983		
	10m	20m	31m	10m	20m	31m	10m	20m	31m
SS									
log a	-6.89	-6.96	-7.24	-7.62	-7.16	-7.50	-7.16	-7.15	-7.90
b	3.17	3.17	3.27	3.52	3.25	3.38	3.31	3.29	3.61
n	56	71	66	45	49	39	24	24	24
r^2	0.94	0.97	0.97	0.95	0.97	0.85	0.99	0.89	0.99
F	903	2513	1909	820	1683	209	1887	183	1864
DB									
log a	-7.37	-7.37	-6.11	-7.26	-7.24	-7.85	-8.86	-8.06	-7.79
b	3.41	3.35	2.72	3.38	3.31	3.57	4.15	3.70	3.56
n	12	22	24	40	29	32	27	29	31
r^2	0.92	0.99	0.84	0.94	0.92	0.93	0.95	0.96	0.95
F	111	1807	118	562	317	415	447	712	551

	6m	16m	6m	16m	6m	16m
Cl						
log a	-7.52	-6.62	-6.61	-6.86	-7.02	-6.47
b	3.39	2.96	3.00	3.08	3.18	2.88
n	71	46	39	35	32	32
r^2	0.97	0.84	0.97	0.93	0.96	0.94
F	2150	225	1196	444	766	487

Table A-27: Parameters and statistics for postspawned gonad weight versus shell height regressions.

SITE	YR	DEP	log a	b	n	r^2	F
TN	82	10m	-6.27	2.85	19	0.72	43
		20m	-5.64	2.50	22	0.77	70
		31m	-5.45	2.33	15	0.69	29
SC	81	10m	-7.92	3.70	44	0.92	453
	82	10m	-5.45	2.63	39	0.61	58
	83	10m	-8.60	4.06	20	0.97	699
SH	83	10m	-7.22	3.38	43	0.95	744
NJ	82	31m	-8.02	3.59	28	0.97	835
	83	31m	-8.60	3.98	24	0.81	96
ST.A	83	10m	-7.05	3.20	40	0.97	1395
		31m	-7.39	3.41	34	0.94	529
		76m	-7.47	3.43	40	0.96	960

Table A-28: Summary of t values for comparisons of prespawned gonad weight versus shell height regressions.

Year											
Dep(m)	Sunnyside		Dildo		TNNP		St.Andrews		Colinet		
1981	a	b	a	b	a	b	a	b	a	b	
10+20	0.1	1.5	0.6	1.2							
20+31	3.0**	1.9	1.4	1.3							
10+31	3.0**	0.9	4.5***	0.0							
6+16									-	3.2*	
1982											
10+20	0.9	0.3	-	2.7**	-	3.7***					
20+31	5.8***	1.8	3.1**	0.3	-	3.8***					
10+31	6.6***	2.0	5.8***	2.3	-	6.5***					
6+16									1.6	1.6	
1983											
10+20	0.2	0.9	0.9	1.5	0.7	0.5					
20+31	5.9***	0.3	-	5.2***	1.1	1.1					
10+31	6.2***	0.9	-	4.0***	1.8	0.7	-	2.8**			
6+16									2.2*	0.5	
10+76							2.3	0.4			
31+76							2.1	2.0			

Table A-29: Summary of t values for comparisons of prespawned gonad weight versus shell height regressions.

Dep(m) Year	Sunnyside+Dildo		Dildo+TNNP		Sunnyside+TNNP	
10m	a	b	a	b	a	b
1981	2.13*	0.31				
1982	-	2.66**	2.69**	1.36	-	5.54***
1983	1.10	1.28	1.03	0.81	2.44*	2.02
20m						
1981	1.57	1.30				
1982	0.46	0.39	4.98***	1.30	6.02***	2.10
1983	0.94	1.53	3.10**	0.75	4.27***	0.43
31m						
1981	3.19**	1.16				
1982	2.12	1.13	0.34	1.22	-	4.04***
1983	5.54***	2.16	-	2.61**	1.72	1.61

Table A-30: Survivorship probabilities used to calculate RRV.

AGE																		
1	1.00																	
2	0.49	1.00																
3	0.37	0.75	1.00															
4	0.34	0.69	0.92	1.00														
5	0.33	0.67	0.89	0.97	1.00													
6	0.33	0.67	0.89	0.97	1.00	1.00												
7	0.32	0.65	0.86	0.94	0.97	0.97	1.00											
8	0.31	0.63	0.83	0.91	0.94	0.94	0.97	1.00										
9	0.29	0.59	0.78	0.86	0.89	0.89	0.91	0.94	1.00									
10	0.26	0.53	0.70	0.77	0.80	0.80	0.82	0.85	0.90	1.00								
11	0.22	0.45	0.54	0.59	0.61	0.61	0.63	0.65	0.69	0.77	1.00							
12	0.18	0.37	0.44	0.48	0.50	0.50	0.52	0.54	0.57	0.64	0.83	1.00						
13	0.14	0.26	0.31	0.34	0.35	0.35	0.36	0.37	0.39	0.44	0.57	0.69	1.00					
14	0.10	0.21	0.25	0.27	0.28	0.28	0.29	0.30	0.32	0.36	0.47	0.57	0.83	1.00				
15	0.08	0.14	0.17	0.18	0.19	0.19	0.20	0.21	0.22	0.25	0.33	0.40	0.58	0.70	1.00			
16	0.05	0.10	0.12	0.13	0.14	0.14	0.15	0.16	0.17	0.19	0.25	0.30	0.44	0.53	0.76	1.00		
17	0.04	0.06	0.08	0.09	0.10	0.10	0.11	0.12	0.13	0.15	0.20	0.24	0.35	0.42	0.60	0.79	1.00	
18	0.02	0.04	0.05	0.06	0.07	0.07	0.08	0.09	0.10	0.12	0.16	0.19	0.28	0.34	0.49	0.65	0.82	1.00
19	0.02	0.03	0.03	0.04	0.05	0.05	0.06	0.07	0.08	0.10	0.13	0.15	0.22	0.27	0.39	0.52	0.66	0.80

Table A-31: Estimates of RRV for the Sunnyside 31m population. Age specific reproductive output values are in brackets.

AGE																		
1																		
2	0.9	(1.9)																
3	2.0	4.0	(5.3)															
4	3.4	6.8	9.1	(9.8)														
5	5.0	10.2	13.5	14.7	(15.1)													
6	6.9	14.1	18.7	20.4	21.0	(21.0)												
7	8.7	17.6	23.3	25.5	26.3	26.3	(27.1)											
8	10.1	20.6	27.2	29.8	30.8	30.8	31.7	(32.7)										
9	11.2	22.8	30.1	33.2	34.3	34.3	35.1	36.3	(38.6)									
10	11.4	23.3	30.7	33.8	35.1	35.1	36.0	37.3	39.5	(43.9)								
11	10.7	21.9	26.3	28.7	29.7	29.7	30.7	31.6	33.6	37.5	(48.7)							
12	9.5	19.6	23.3	25.4	26.5	26.5	27.5	28.6	30.2	33.9	43.9	(52.9)						
13	8.0	14.8	17.7	19.4	19.9	19.9	20.5	21.1	22.2	25.0	32.4	39.3	(56.9)					
14	6.0	12.6	15.0	16.2	16.8	16.8	17.4	18.0	19.2	21.6	28.3	34.3	49.9	(60.1)				
15	5.1	8.9	10.8	11.4	12.0	12.0	12.7	13.3	13.9	15.8	20.9	25.3	36.7	44.3	(63.3)			
16	3.5	6.3	7.9	8.6	9.3	9.3	9.9	10.6	11.2	12.5	16.5	19.8	29.0	35.0	50.1	(66.0)		
17	2.5	4.3	5.4	6.1	6.8	6.8	7.5	8.2	8.8	10.2	13.6	16.3	23.9	28.6	40.9	53.8	(68.1)	
18	1.7	3.0	3.5	4.2	4.9	4.9	5.6	6.3	7.1	8.5	11.3	13.4	19.7	24.0	34.5	45.8	57.8	(70.5)
19	1.2	2.0	2.2	2.9	3.6	3.6	4.3	5.0	5.8	7.2	9.3	10.8	15.8	19.4	28.0	37.4	47.4	57.5
	107.7	212.6	264.6	280.3	277.1	256.1	238.9	216.3	191.5	172.2	176.3	159.2	175.0	151.2	153.6	137.0	105.2	57.5

Table A-32: Estimates of RRV for the Sunnyside 10m population. Age specific reproductive output values for 1982 are in brackets.

AGE																	
2	0.7	(1.5)															
3	3.1	6.2	(8.3)														
4	8.3	16.9	22.5	(24.5)													
5	16.4	33.3	44.3	48.2	(49.7)												
6	27.1	55.1	73.2	79.9	82.2	(82.2)											
7	38.1	77.4	102.5	112.0	115.6	115.6	(119.2)										
8	49.4	100.4	132.2	144.9	149.8	149.8	154.6	(159.3)									
9	57.8	117.5	155.4	171.3	177.3	177.3	181.3	187.3	(199.2)								
10	61.9	126.3	166.8	183.5	190.7	190.7	195.4	202.6	214.5	(238.3)							
11	60.2	123.2	147.8	161.5	167.0	167.0	172.4	177.9	188.9	210.8	(273.7)						
12	55.3	113.8	135.3	147.6	153.7	153.7	159.9	166.0	175.3	196.8	255.2	(307.5)					
13	47.1	87.5	104.3	114.4	117.8	117.8	121.1	124.5	131.2	148.1	191.8	232.5	(336.5)				
14	36.3	76.2	90.7	98.0	101.6	101.6	105.2	108.8	116.1	130.6	170.5	206.8	301.1	(362.8)			
15	30.9	54.0	65.6	69.5	73.3	73.3	77.2	81.1	84.9	96.5	127.4	154.4	223.9	270.2	(385.9)		
16	21.5	38.6	48.8	52.8	56.9	56.9	61.0	65.0	69.1	77.2	101.6	121.9	178.8	215.4	308.9	(406.4)	
17	15.2	26.7	33.9	38.1	42.3	42.3	46.6	50.8	55.0	63.5	84.7	101.6	148.2	177.9	254.1	334.5	(423.5)
18	18.4	18.4	21.9	26.3	30.6	30.6	35.0	39.4	43.8	52.5	70.0	83.1	122.5	148.8	214.4	284.4	358.8 (437.6)
19	7.2	12.6	13.4	18.0	22.5	22.5	27.0	31.5	36.0	45.1	58.6	67.6	99.1	121.7	175.7	234.3	297.4 360.5
	555	1,084	1,359	1,466	1,481	1,399	1,337	1,235	1,115	1,021	1,060	968	1,074	934	953	853	656 361

Table A-33: Estimates of RRV for the Sunnyside 10m population. Age specific reproductive output values for 1981/83 are in brackets.

AGE																	
2	1.6	(3.3)															
3	4.3	8.8	(11.70)														
4	8.7	17.6	23.5	(25.5)													
5	13.9	28.2	37.4	40.8	(42.0)												
6	19.8	40.1	53.3	58.1	59.9	(59.9)											
7	25.6	52.0	68.7	75.1	77.5	77.5	(79.9)										
8	29.8	60.5	79.7	87.4	90.3	90.3	93.1	(96.0)									
9	32.6	66.4	87.8	96.8	100.1	100.1	102.4	105.8	(112.5)								
10	33.2	67.7	89.4	98.3	102.1	102.1	104.7	108.5	114.9	(127.7)							
11	31.0	63.4	76.1	83.2	86.0	86.0	88.8	91.6	97.3	108.6	(141.0)						
12	27.5	56.6	67.3	73.4	76.5	76.5	79.5	82.6	87.2	97.9	126.9	(152.9)					
13	22.8	42.4	50.5	55.4	57.1	57.1	58.7	60.3	63.6	71.7	92.9	112.5	(163.1)				
14	17.2	36.1	43.0	46.5	48.2	48.2	49.9	51.6	55.1	62.0	80.9	98.1	142.8	(172.1)			
15	14.4	25.2	30.6	32.4	34.2	34.2	36.0	37.8	39.6	45.0	59.3	71.9	104.3	125.9	(179.8)		
16	9.9	17.7	22.4	24.3	26.1	26.1	28.0	29.9	31.7	35.5	46.7	56.0	82.2	99.0	141.9	(186.7)	
17	6.9	12.1	15.4	17.3	19.2	19.2	21.2	23.1	25.0	28.8	38.5	46.2	67.3	80.8	115.4	151.9	(192.3)
18	4.7	8.3	9.8	11.8	13.8	13.8	15.7	17.7	19.7	23.6	31.5	37.3	55.0	66.8	96.3	127.8	161.2 (196.6)
19	3.2	5.6	6.0	8.0	10.0	10.0	12.0	14.1	16.1	20.1	26.1	30.1	44.2	54.2	78.3	104.4	132.5 160.7
Σ	307	609	761	809	801	741	690	623	550	493	503	452	496	427	432	384	294 161